

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



Volume 64

1999

Wissenschaftliche Originalarbeiten

Wissenschaftliche Kurzmitteilungen

Printed in Germany

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

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ISSN 0044-3468 · Z. Säugetierkunde · 64(1999)1 · S. 1-64 · Februar 1999

URBAN & FISCHER

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1999

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Z. Säugetierkunde **64** (1999) 1–11



ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Morphological and colour variation in the Pyrenean desman *Galemys pyrenaicus* (Geoffroy, 1811)

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Receipt of Ms. 10. 03. 1998
Acceptance of Ms. 18. 11. 1998

Abstract

This study presents information on biometry and colouring of *Galemys pyrenaicus*. The material studied covers the entire distribution area of this species on the Iberian Peninsula. Based on the data examined, no significant geographic differences were found as far as skull size was concerned. However, skull sizes and some of the body measurements taken from animals native to the Pyrenees and included in the subspecies *pyrenaicus*, are intermediate between subspecies from Galicia and the Iberian Mountains, and included in the subspecies *rufulus*. These data diminish some of the validity accorded to craniometric measures as one criterion to justify the existence of subspecies. Colour allows for a better differentiation although the chorological patterns do not coincide with those established by other authors. We suggest that *Galemys pyrenaicus* is distributed in totally or partially isolated populations, which could favour the process of morphological differentiation. This emphasises the importance of preserving every population area of this species.

Key words: *Galemys pyrenaicus*, taxonomy, morphology, colour

Introduction

Since the first description of this species by GEOFFROY (1811) in the last century, and description by GRAELLS (1897), sufficient differences in coloration have been seen between the typical form and the desmans from the central Iberian Peninsula in order to consider the latter as a new variety. Only in studies by six authors (MILLER 1912; CABRERA 1914; NIETHAMMER 1970; PALMEIRIN and HOFFMANN 1983; JUCKWER 1990) has there been any mention of the variability in form and size seen in the desman *Galemys pyrenaicus* in its distributional area.

GEOFFROY (1811) described the dorsal fur as being dark brown ("brun marron") in colour. Years later GRAELLS (1897) based his new variety, *Myogalea rufula*, noting that the yellow colour of the hairs on the back renders the animal to appear to have gold reflexes, while in the type specimen these reflexes appear silver. He also reported as a distinguishing trait, the bright yellow colour of the paws and nails of the desmans from the Central Mountains.

MILLER (1912) described the coloration of *Galemys pyrenaicus rufulus* as not as dark as that of the subspecies of the Pyrenees. This author reports that the form *rufulus* appears to be clearly differentiated from *pyrenaicus* owing to its larger size and especially to the greater length and strength of the skull.

0044-3468/99/64/01 – 001 $ 12.00/0

Cabrera (1914) did not find any substantial differences in coloration between the two forms and he even claimed that the original description of *rufulus* was totally useless for recognising the animal in question. He did, however, maintain the existence of two subspecies attributing the bulk of the differentiation to the size; indicating, as discriminating parameters, the length of the rear foot and the condylobasal length.

Niethammer (1970) cautioned that although the form *rufulus* is larger in size, the measurements do overlap. He also pointed out that fur colour varies depending on wear.

Palmeirin and Hoffmann (1983) considered that the subspecies are distinct, although morphological differences between them are not great.

Lastly Juckwer (1990), through the examination of body weight and condylobasal length, attempted to reaffirm the idea that the subspecies *rufulus* is greater in size than the subspecies *pyrenaicus*.

The purpose of this study is to provide information on the biometry and coloration of the desman, analyse the geographic variation of this species on the Iberian Peninsula and discuss its present taxonomic status.

Material and methods

The material studied consisted of all together specimens from different collections (Tab. 1). In addition we used biometric data provided by Miller (1912), n = 6; Niethammer (1970), n = 18; Juckwer (1990), n = 20 (Tab. 1). It is important to note that material from the Central Mountains was not available. The presumable precariousness of the populations living in these mountains made it inadvisable to collect material there.

In order to evaluate the geographic variation of the size, the specimens were divided into 5 groups (Fig. 1).

Table 1. Origin and composition of the material. Sources: 1 – Museo Luis Iglesias, 2 – Estación Biológica de Doñana, 3 – Museo de Ciencias Naturales, (Alava), 4 – Collection from Pablo Aguirre, 5 – Facultad de Biología, Universidad de León, 6 – Museo Luis Iglesias (Santiago de Compostela), 7 – Niethammer (1970), 8 – Miller (1912), 9 – Juckwer (1990), 10 – own material

Population	Province	Location	U. T. M.	Skull	Fur	Source
Occidental 1	La Coruña:	–	–	–	1	1
	Lugo:	Trascastro-Incio	29TPH32	5	–	2
		Saa de Incio	29TPH32	8	–	2
		San Pedro de	29TPH32	5	–	2
		Incio	29TPH32	10	–	2
		San Román	29TPH54	1	–	6
		Cadramón	29TPJ10	1	–	6
		Barbeitos	29TPH67	1	–	6
		Río Ulla		1	1	1
	Pontevedra:	Río Riobó		1	1	1
		Vila de Cruces	29TNH63	–	1	1
	Orense:	Xunqueira de	29TPG07	1	–	6
		Sierra de	29TPG36	1	–	6
		Ramirás	29TNG77	1	–	6
		Riobó	29TPG26	1	–	6
	León:	Matarrosa del Sil	29TQH03	3	–	2
		Paramo del Sil	29TQH04	2	–	2
		Peranzanes	29TPH95	2	–	2
		Manzaneda	29TQG28	2	–	2
		Sierra Cabrera	29TPG97	1	–	2
		Montrondo	29TQH24	1	1	2

Table 1. Continued

Population	Province	Location	U. T. M.	Skull	Fur	Source
Occidental 2	Asturias:	Pola de Somiedo	29TQH27	4	–	2
		Arriondas	30TUP20	2	–	2
		Caleao	30TUN08	1	1	10
	Cantabria:	Turieno	30TUN67	4	–	2
		Rio Quiviesa	30TUN67	1	–	2
		Rio Hijar	30TUN96	1	–	2
		Reinosa	30TVN06	2	–	2
		Espinama	30TUN57	3	–	2
	León:	Besande	30TUN45	1	–	2
		Candemuela	29TQH46	6	7	10
		Riano	30TUN35	1	–	7
		Pajares	30TTN76	1	–	8
		San Emiliano	29TQH46	1	1	10
Pyrenees	Navarra:	Burguete	30TXN36	6	–	7
		Quinto Real	30TXN26	50	49	10
		Aoiz	30TXN34	1	1	10
		Orbara	30TXN45	1	1	10
		Oroz-Betelu	30TXN35	1	–	10
		Saigos	30TXN25	1	–	10
		Akerreta	30TXN15	1	–	10
		Lanz	30TXN16	2	–	10
		Huizi	30TWN87	2	–	10
		Oricain	30TXN14	1	–	10
		Riba	30TXN15	1	–	10
		Itoiz	30TXN34	1	–	10
		Osteriz	30TXN25	1	–	10
		Garzaron	30TWN96	2	–	10
		Guerendain	30TXN05	1	–	10
	Álava:			–	2	3
Iberian	Burgos:	Santo Domingo de	30TVM64	1	–	2
		Santo Domingo de	30TVM64	5	–	8
	La Rioja:	Sierra de Cameros	30TWM27	3	–	7
		Sierra de Cameros	30TWM27	20	–	9
		Ajamil	30TWM46	1	1	4
		Peroblasco	30TWM67	1	1	4
		Aguillar de Río	30TWM84	1	1	4
		Vadillos	30TWM47	1	1	4
		Valdepecillo	30TWM75	1	1	4
Central	Ávila:	Sierra de Gredos	30TTK95	8	–	7

The following measurements were studied: Body: HBL (head + body length), TL (tail length), HFL (hind foot length) W (body weight in grams); cranium: CBL (condyle-basal length), I^1–M^3 (I^1–M^3 length), BW (skull case width), IOW (interorbital width), ML (mandibular length), CH (coronoid height), BH (skull case height). The CBL was measured following Juckwer (1990). Since the points used by this author to define this parameter do not coincide with those used by Miller (1912) and Niethammer (1970) this study did not rely on the LCB measurements given by the latter authors.

The relative size was assessed according to Grulich (1967) for *Talpa*, taking into account tooth wear. Although all the teeth suffer from deterioration, it is more visible in the incisors, canines, and premolars. Animals with the cusps of teeth intact or only little evidence of wear were considered young. Animals showing abrasion down to the middle of the crowns were considered adults, and those that had a highly deteriorated set of teeth – in some cases the crown was completely lacking – were considered old adults. Where possible, characteristics of the reproductive system, such as size and degree of development were taken into account to supplement the age criteria.

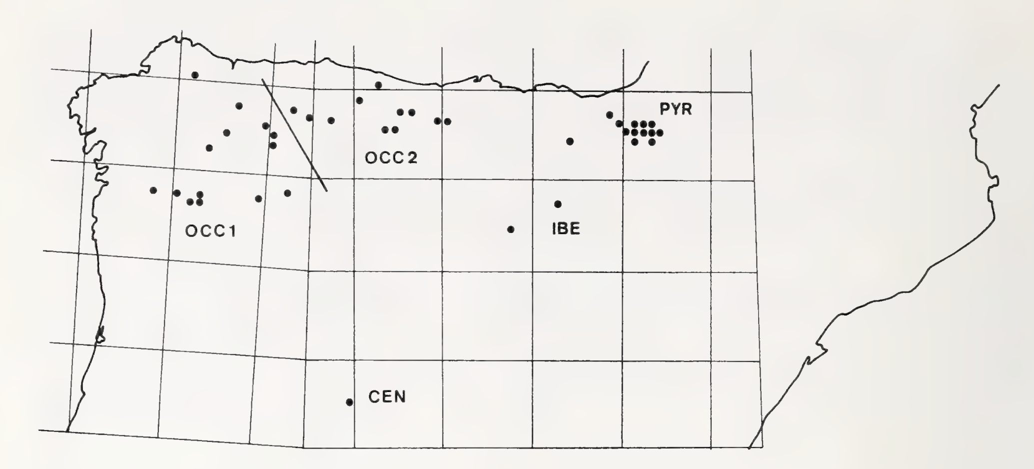


Fig. 1. Study area and different population groups. Occ1: animals from Galicia and the west of the province of León; Occ2: animals from Asturias, Cantabria, and the north of the province of León; Pyr: animals from Navarra; Ibe: animals from La Rioja and the south of the province of Burgos; Cen: animals from the province of Ávila

In order to evaluate the geographic variation of coloration, only those animals were considered showing new fur or fur grown after the moult. Thus, we counted 5 specimens from the Occidentall population, 9 from Occidental 2, 17 from the Pyrenees, and 5 from the Iberian Mountains.

The normality of the distribution of the variables was determined by the Kolmogorov-Smirnov test (Nie et al. 1975). The comparison between mean sampling pairs was carried out according to the method of Scheffé (Nie et al. 1975). The degree of differentiation between the different groups in terms of sex, age, and season of the year that the animal was caught was estimated based on the set of variables chosen through the multivariate analysis of variance (MANOVA) (Nie et al. 1975). The geographic variation of size was evaluated by a step-by-step discriminating factorial analysis choosing the variables which maximise the D^2 of Mahalanobis between the two closest groups (Nie et al. 1975).

Results

Size

Morphometric and craniometric data of the populations are given in table 2. An analysis of the total variability of the parameters considered resulted in no differences concerning size that may be attributed to sex (T^2 from Hotellings = 0.794; F = 1.192; $p > 0.05$), age (T^2 from Hotellings = 1.914; F = 1.355; $p > 0.05$), or season (T^2 from Hotellings = 3.058; F = 1.416; $p > 0.05$).

Individual comparisons between pairs of samples (Tab. 3) indicate that desmans from the Occidental 1 population have smaller skulls. This is the group that has the greatest number of contrasts with significant differences of several measures (18 out of 22 comparisons). As far as body measurements are concerned, the Iberian group has the lowest values. However, from the comparisons it is not possible to establish a clear pattern of geographic variation of these parameters.

A preliminary discriminating analysis was carried out based on five craniometric variables (CBL, I^1–M^3, BW, IOW, ML) and on the first four groups considered (OCC.1, OCC.2, PYR., IBER.). The discriminating function which explains a greater percentage of the variance (66.83%) selects four variables: $D = (-0.063) \times CBL + (1.091) \times I^1\text{–}M^3 + (-1.498) \times IOW + (2.189) \times ML - 54.384$. The standardised coefficients of this function

Table 2. Morphometric (in mm and grams) and craniometric (in mm) values of the populations studied

		n	$\overline{X}$	S	min.	max.
CBL	OCC1	50	33.8	1.22	29.4	35.5
	OCC2	15	34.8	0.60	33.8	36.0
	PYR	67	34.4	0.57	33.0	35.5
	IBE	26	34.9	0.57	34.1	36.2
	CEN	–	–	–	–	–
I^1–M^3	OCC1	50	16.6	0.66	14.8	17.8
	OCC2	15	17.1	0.29	16.6	17.8
	PYR	67	16.7	0.34	15.9	17.7
	IBE	26	17.0	0.24	16.3	17.3
	CEN	–	–	–	–	–
BW	OCC1	50	16.1	0.58	14.9	17.5
	OCC2	21	16.6	0.52	15.6	17.5
	PYR	67	16.4	0.34	15.7	17.2
	IBE	30	16.7	0.45	15.5	17.8
	CEN	–	–	–	–	–
IOW	OCC1	50	6.1	0.25	5.3	6.6
	OCC2	21	6.4	0.22	6.0	6.8
	PYR	67	6.4	0.21	6.0	7.0
	IBE	31	6.2	0.23	5.9	6.8
	CEN	–	–	–	–	–
BH	OCC1	50	10.8	0.50	9.2	12.0
	OCC2	15	11.1	0.45	10.5	11.8
	PYR	67	11.2	0.27	10.5	11.8
	IBE	6	11.5	0.15	11.2	11.6
	CEN	–	–	–	–	–
ML	OCC1	25	21.5	0.63	19.7	22.7
	OCC2	15	22.0	0.46	20.9	22.6
	PYR	66	21.7	0.38	20.7	22.6
	IBE	30	22.3	0.52	21.6	24.0
	CEN	–	–	–	–	–
CH	OCC1	25	10.4	0.31	10.0	11.0
	OCC2	14	10.8	0.45	9.9	11.5
	PYR	67	10.8	0.33	10.0	11.5
	IBE	5	10.8	0.21	10.5	11.0
	CEN	–	–	–	–	–
HBL	OCC1	6	122.8	13.70	110	145
	OCC2	19	125.6	5.38	112	135
	PYR	68	121.9	6.67	104	133
	IBE	29	116.1	6.68	106	129
	CEN	8	116.5	6.39	108	125
TL	OCC1	5	138.4	5.08	135	147
	OCC2	19	143.2	9.53	113	156
	PYR	68	139.7	6.54	123	154
	IBE	29	137.6	8.99	118	156
	CEN	8	148.1	5.94	140	155
HFL	OCC1	6	33.9	0.97	32.5	35.0
	OCC2	19	34.9	1.32	31.0	36.5
	PYR	68	35.4	1.07	31.0	37.5
	IBE	29	34.5	1.21	32.5	36.9
	CEN	8	33.9	0.88	32.5	35.0
W	OCC1	3	66.0	3.46	64	70
	OCC2	11	76.0	3.90	70	81
	PYR	66	68.6	7.38	48	83
	IBE	29	65.5	8.27	51	80
	CEN	8	68.4	7.73	60	79

Table 3. Individual comparisons between pairs of samples for each variable analysed according to the method of Scheffe. OCC1: Occidental 1 population; OCC2: Occidental 2 population; PYR: Pyrenean population; IBE: Iberian population; CEN: central population. The probability of error is noted when there are significant differences. * = No significant differences. – = Test was not carried out (sample size less than 5).

	OCC1–OCC2	OCC1–PYR	OCC1–IBE	OCC1–CEN	OCC2–PYR	OCC2–IBE	OCC2–CEN	PYR–IBE	PYR–CEN	IBE–CEN	Minor to highest size				
CBL	0.05	0.05	0.05	–	*	*	–	*	–	–	OCC1	PYR	OCC2	IBE	
$I^1–M^3$	0.05	*	0.05	–	0.05	*	–	*	–	–	OCC1	PYR	IBE	OCC2	
BW	0.05	0.05	0.05	–	*	*	–	*	–	–	OCC1	PYR	OCC2	IBE	
IOW	0.05	0.05	*	–	*	*	–	0.05	–	–	OCC1	IBE	OCC2	PYR	
BH	0.05	0.05	0.05	–	*	*	–	*	–	–	OCC1	OCC2	PYR	IBE	
ML	0.05	*	0.05	–	*	*	–	0.05	–	–	OCC1	PYR	OCC2	IBE	
CH	0.05	0.05	*	–	*	*	–	*	–	–	OCC1	PYR	IBE	OCC2	
HBL	*	*	*	*	*	0.05	0.05	0.05	*	*	IBE	CEN	PYR	OCC1	OCC2
TL	*	*	*	*	*	*	*	*	*	0.05	IBE	OCC1	PYR	OCC2	CEN
HFL	*	*	*	*	*	*	*	0.05	0.05	*	CEN	OCC1	IBE	OCC2	PYR
W	–	–	–	–	0.05	0.05	*	*	*	*	IBE	CEN	PYR	OCC2	

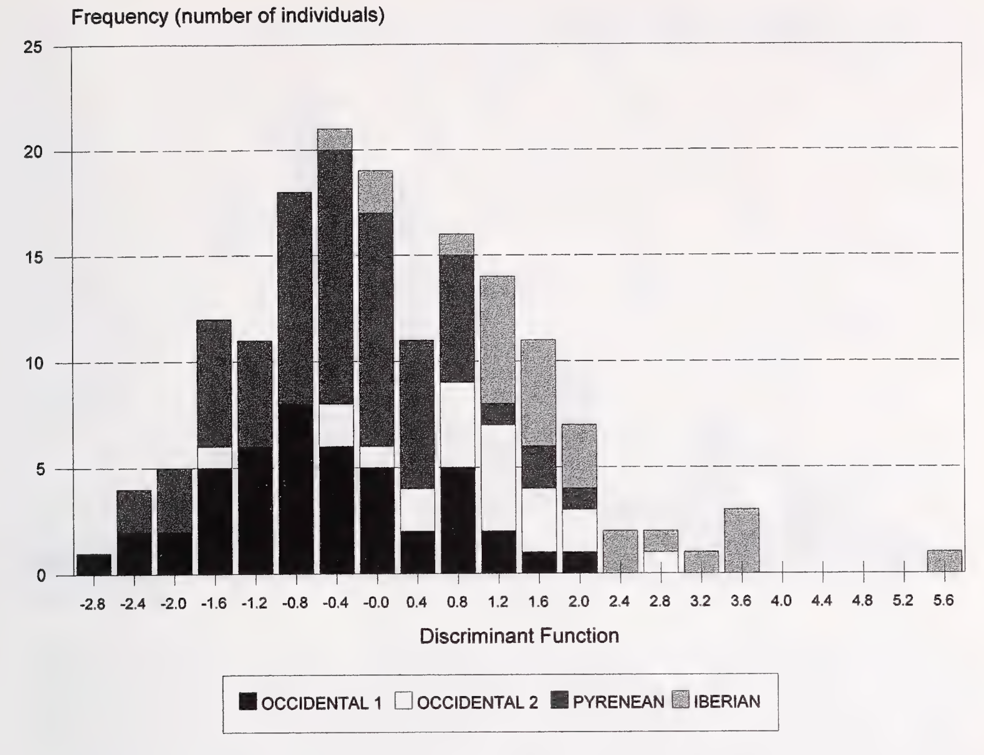


Fig. 2. Distribution of the sample analysed according to the discriminating function considering five craniometric sizes (CBL, I^1–M^3, BW, IOW, ML)

(ML = 0.86; I^1–M^3 = 0.46; IOW = –0.33; CBL = –0.04) and the correlation coefficients between the variables and the function (ML = 0.89; I^1–M^3 = 0.54; IOW = 0.01; CBL = 0.57) highlight I^1–M^3 and ML as the variables with the greatest discriminating power. Although their significance reaches a value which is high enough to warrant attention (Lambda de Wilks = 0.623, $p < 0.001$), it should be noted that only 61.6% of the sample (Fig. 2) is accurately classified. According to the data obtained, there is a wide overlap between the groups under comparison. The ordination of the centroid values of the groups situates the Occidental 1 (–0.61) and Pyrenean (–0.45) populations on the negative side of the function and the Occidental 2 (0.77) and Iberian (1.62) populations on the positive side. Since I^1–M^3 and ML have a positive correlation with the function, this ordination highlights the smaller skull size of the animals from Occidental 1 and Pyrenean populations.

A second discriminating analysis was carried out, adding the body parameters HFL, HBL, and TL to the variables used in the first analysis. In this case only the animals from the Occidental 2, Iberian, and Pyrenean populations presented complete information of the parameters under consideration. The discriminating function which explains a higher percentage of variance (89.6%) makes a selection of seven variables: $D = (-0.81) \times CBL + (-1.57) \times I^1–M^3 + (2.07) \times IOW + (-1.41) \times ML + (0.91) \times HFL + (0.04) \times TL + (0.05) \times HBL + 29.04$. The standardized coefficients of this function (ML = –0.56; I^1–M^3 = –0.43; IOW = 0.45; CBL = –0.44; HFL = 0.78; TL = 0.23; HBL = 0.29) and the correlation coefficients among the variables as well as the function (ML = –0.41; I^1–M^3 = –0.33; IOW = 0.18; CBL = –0.25; HFL = 0.36; TL = 0.21; HBL = 0.30) point to I^1–M^3, ML, CBL, IOW, and HFL as the parameters with the greatest discriminating power.

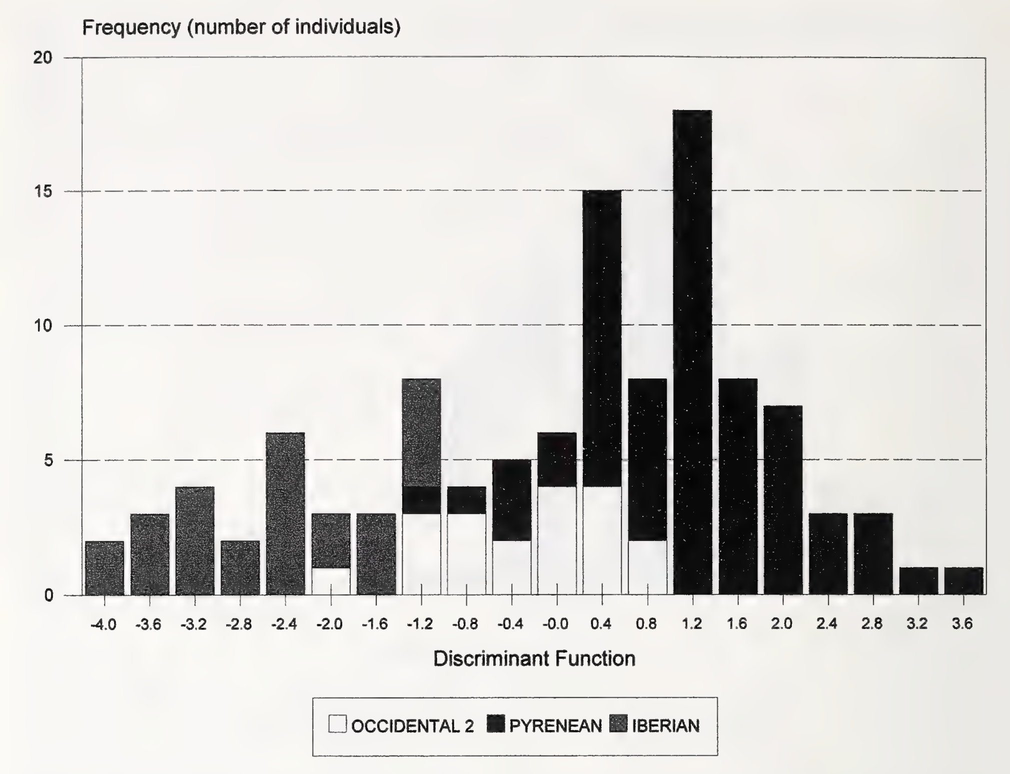


Fig. 3. Distribution of the sample analysed according to the discriminating function considering five craniometric sizes (CBL, I^1–M3, BW, IOW, ML) plus three body sizes (HFL, HBL, TL)

In this case the efficiency of the function obtained is relatively high since it provides an accurate classification percentage, 87.3% (Fig. 3). The ordination of the centroid values of the groups places the Iberian population on the negative side of the function (–2.82) and the Pyrenean population on the positive side (1.25), while the Occidental 2 population is intermediate in location (–0.44). Since the selected skull lengths correlate negatively with the function and IOW and HFL have a positive correlation, this ordination assigns a shorter and stronger skull and longer foot to the Pyrenean population as compared to the Iberian population.

Fur coloration

Based on an examination of all the pelts taken from the Quinto Real (Navarra), no differences in coloration were noted among the three relative age classes, if we compare animals caught during the same season. However, differences were seen upon comparing animals of the same age caught during different seasons. This is due to the wear the guard hairs are subject to (in the desman there are two types of guard hairs, the most common being the ones Poduschka and Richard (1985) call "Grannen"). After examining these hairs under the light microscope, the distal ends were seen to be intact and the coloration at first glance appears to be uniformly dark brown in young animals that have just grown a coat of fur or in adults that have recently moulted (animals caught between July and September). In contrast, in animals caught between January and March there are fine yellowish spots on the back. These spots are the distal ends of the "Grannen". With the light

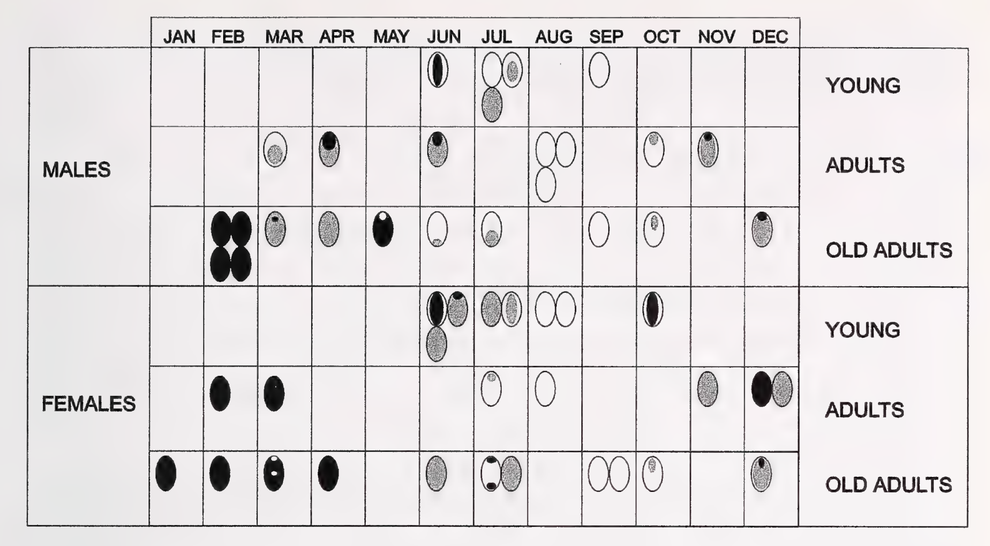


Fig. 4. Distribution of the area mottled in the dorsal fur. The darkest zones represent a greater yellowish spot density. The studied individuals appear distributed in function of their relative age and their month of capture

microscope it can be seen that these ends are split and appear dark and soiled. This worn fur has a yellowish tint at first glance, which corresponds to the spots seen in the old, worn fur. The notion that this variation in coloration is due to the deterioration of the fur was corroborated, when the group of pelts was arranged by months of capture and age (Fig. 4). The distribution of the dorsal spots and the temporal sequence observed would suggest that the moulting of the dorsal fur follows a regular pattern and is completed in August and September.

The coloration of the ventral part has a similar evolution. In June–August when the animal has new fur, the ventral part is white in colour; as the fur gets older it starts turning yellow (with gold spots). No differences were seen between the sexes in terms of fur coloration.

On comparing fur coloration between the established groups of animals, the colour of the ventral part did not show any substantial differences. It could be described as a shiny greyish white. The colour of the dorsal fur, however, differed among specimens of the different groups. The animals from the Pyrenean population have a dark brown colouring, which in some cases is almost black. The animals from the Iberian population have a similar dorsal colouring, although slightly lighter. The animals belonging to the Occidental 2 population have a reddish dorsal colouring, which is considerably lighter and they are the only specimens having yellow forepaws, feet, and nails. The latter fits the description that Graells (1897) gave of the subspecies *rufulus*. The animals from the Occidental 1 population have a light coloration similar to those of Occidental 2 with the exception of one specimen which is slightly darker. In specimens having dry fur it was not possible to detect differences in shade between the worn fur of the different groups studied.

Discussion

Based on the data analysed it is difficult to find structured patterns in relation to skull size. The craniometric values of the animals from the Pyrenees, described as *pyrenaicus*,

are intermediate between the specimens from Galicia and the Iberian range, both described as *rufulus*, which would discredit the opinion of MILLER (1912) and CABRERA (1914) who based the discrimination of the subspecies on size.

The fur coloration does, however, show geographic differences, which would contradict, in this case, CABRERA's (1914) opinion. The animals from the Pyrenees, Basque Country and the Iberian Range are dark brown (blackish) in colour, while the animals from the occidental area (León, Asturias, Galicia) belong to the light brown (reddish) type. The spots in the fur alluded to by GRAELLS (1897) are due to the deterioration of the fur.

In its distribution area *Galemys pyrenaicus* presents a morphological variability that does not allow a clear differentiation to be made between the two subspecies described. It is only the coloration that fits a general geographic pattern, distinguishing the specimens from the Pyrenees and Iberian Range from the remainder, although within each of the two groups there is still a certain degree of heterogeneity. The morphometric and colouring observations obtained do not support the distributions of the two subspecies as described in the bibliography.

Thus, the distribution of the population variations would be more complicated than the simple description of the two known subspecies. The desman is a species linked to the high regions of the rivers (CASTIÉN and GOSÁLBEZ 1992). The dispersive characteristics of this species have not been examined to date, but dispersion is certain to be basically related to river courses. This would lead us to state that total or partial isolation between the populations of this species is a common occurrence. Moreover, if we add the territorial character of these animals and their low density (STONE 1987), it would be possible to consider that genetically related phenomena occur. The existence of these phenomena may explain the presence of local variations throughout the distribution area of the species. An in-depth genetic study would make it possible to establish the taxonomic importance of these variations in the future.

Acknowledgements

The authors would like to thank PABLO AGIRRE-MENDI, GORKA BELAMENDIA (Museo de Ciencias Naturales de Álava), Estación Biológica de Doñana (Sevilla), Museo Luis Iglesias (Santiago de Compostela) and Dr. FRANCISCO J. PURROY (Facultad de Biología de León) for kindly providing the material studied. The authors are also grateful to I. LERÁNOZ for her generous help in the collection of our own material. This study was partially funded by the Secció de Ciencies Biologiques de l'Institut d'Estudis Catalans (Barcelona).

Zusammenfassung

Morphologische und Färbungsvariationen beim Pyrenäen-Desman Galemys pyrenaicus (Geoffroy, 1811)

Die Arbeit enthält Angaben über Biometrie und Färbung des Pyrenäen-Desman *Galemys pyrenaicus*. Die Autoren untersuchen die geographische Variation der Größe und Färbung dieser Art innerhalb der Iberischen Halbinsel und kommentieren den derzeitigen taxonomischen Wissensstand. Das untersuchte Material bezieht sich auf alle Regionen der Iberischen Halbinsel, in denen diese Art vorkommt. Die Ergebnisse dieser Analyse zeigten in bezug äuf die Schädelgröße keine bedeutenden geographischen Unterschiede. Sowohl die Schädelgröße als auch einige andere Körpermaße der in den Pyrenäen lebenden Unterart *pyrenaicus* liegen zwischen den Maßen der in Galicien und dem Iberischen Gebirge lebenden Unterart *rufulus*. Dieses Ergebnis stellt die Heranziehung der Schädelgröße als Maßstab für die Unterscheidung von Unterarten in Zweifel. Eindeutigere Unterscheidungsfaktoren bestehen bezüglich der Farbe, allerdings stimmen hierbei die chorologischen Modelle nicht mit

denjenigen anderer Autoren überein. Die vorliegende Studie legt nahe, daß die einzelnen Populationen von *Galemys pyrenaicus* zum Teil oder gänzlich isoliert sind, wodurch eine morphologische Unterscheidung begünstig sein kann. Diese Tatsache hebt die Notwendigkeit der Erhaltung jedes einzelnen dieser Siedlungskerne hervor.

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INTERNATIONAL JOURNAL
OF MAMMALIAN BIOLOGY

Eine spezielle Markierungsweise und ihre strukturelle Grundlage beim Krabbenwaschbär (*Procyon cancrivorus*)

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Eingang des Ms. 30. 03. 1998
Annahme des Ms. 23. 07. 1998

Abstract

A specific type of scent marking and its structural basis in the Crab-eating raccoon (Procyon cancrivorus)

The study describes for the first time rubbing of the nuchal region as a normal form of behaviour as well as a frequently applied territorial scent marking in the crab-eating raccoon (*Procyon cancrivorus*). Different objects marked with a fatty and odorous secretion by typical rotating or vertical movements of the head were olfactorily controlled by other members of the group studied. Concerning the fur, in contrast to the normal backwards orientated hairs at the dorsum those in the nuchal region with their tips pointed toward the head or straight upward. A histological analysis of the nuchal integument exhibited, as compared to the dorsal body region, a thickening of the cutis, distinctly enlarged sebaceous glands and apocrine tubular glands of central primary hair follicles producing the heavy guard hairs. These hair follicles were increased in length but not in thickness.

The possible biological function of this "glandular organ" of the nuchal region in the crab-eating raccoon is discussed.

Key words: *Procyon cancrivorus*, nuchal integument, scent marking

Einleitung

Innerhalb der Familie der Neuwelt-Kleinbären (Procyonidae) ist der nordamerikanische Waschbär (*Procyon lotor*) die wohl am häufigsten untersuchte Spezies. Weitaus geringer sind die Kenntnisse zur Biologie des engsten Verwandten, des südamerikanischen Krabbenwaschbären (*Procyon cancrivorus*). Nur wenige Arbeiten, wie z. B. diejenige von Yanosky und Mercolli (1993), die den jahreszeitlichen Aktivitätsrhythmus von Krabbenwaschbären im El Bagual Ecological Reserve von Nord-Argentinien darstellt, geben dabei Auskunft über das Verhalten dieser Tiere. Bedingt durch die dämmerungs- und nachtaktive Lebensweise der Krabbenwaschbären lassen sich jedoch differenzierte ethologische Studien im Freiland nur in begrenztem Umfang durchführen. Aus diesem Grund wurden in der vorliegenden Arbeit die Verhaltensmuster von in Gehegehaltung lebenden Tieren beider Geschlechter näher analysiert. Dabei konnte eine für Krabbenwaschbären bisher noch nicht beschriebene Verhaltensweise des Markierens gefunden werden, für deren strukturelles Korrelat im Integument ebenfalls noch keine Informationen vorlagen.

0044-3468/99/64/01 – 012 $ 12.00/0

Material und Methode

Von sechs im Gehege des Instituts für Zoologie der Tierärztlichen Hochschule Hannover gehaltenen subadulten und adulten Krabbenwaschbären (*Procyon cancrivorus nigripes* Mivart, 1886) (1 ♂; Alter 9 Jahre; 5 ♀♀; Alter 2, 6, 11 Jahre; Leihgaben des Zoo São Paulo, Brasilien) wurde das Verhalten über einen Zeitraum von 14 Monaten beobachtet, wobei die „one-zero-sampling" Methode zur Anwendung kam. Für jedes einzelne Tier wurde dabei monatlich ein 24 h-Tag protokolliert (Martin und Bateson 1992).

Von einem weiblichen (3 Jahre) und einem männlichen Tier (11 Jahre), die durch Krankheit bedingt (Bißverletzung, Tumorerkrankung) euthanasiert werden mußten, war es möglich, mehrere Hautproben aus der Nackenregion sowie dem gesamten Rückenbereich zu entnehmen. Das Material wurde in Bouinscher Lösung fixiert und nach Entwässerung über eine aufsteigende Ethanol-Reihe in den Kunststoff Technovit 7100 (Fa. Kulzer) eingebettet (Gerrits und Smid 1983). Dieses Glykolmethakrylat-Gemisch verursacht keine Schrumpfungsartefakte (Hanstede und Gerrits 1983) und läßt sich daher gut für Vermessungen am histologischen Schnitt verwenden. Nach der Herstellung von 3 µm dicken Schnitten am Autocut-Mikrotom (Fa. Reichert-Jung) wurden diese mit Hämatoxylin (Hämalaun nach Delafield) – Eosin oder 1%igem Toluidinblau (nach Richardson et al. 1960) gefärbt.

Vermessungen verschiedener Hautanteile erfolgten an je fünf bis acht histologischen Schnitten von je sechs Proben aus dem Nacken und je sechs bis acht Proben aus der Rückenregion mit Hilfe eines standardisierten Zeichengeräts (Fa. Zeiss). Die Mittelwerte der Meßergebnisse zur Hautdicke sowie von 10 bis 15 zentralen Primärhaarfollikeln und ihren Anhangsdrüsen je Hautprobe wurden auf Normalverteilung und mit Hilfe des t-Tests nach Student anschließend auf signifikante Unterschiede überprüft.

Ergebnisse

Im Rahmen ihres Territorialverhaltens markierten die Krabbenwaschbären im Gehege regelmäßig mit Hilfe des Analbeutelsekrets und durch Abgabe kleinerer Harnmengen. Auffallend war zusätzlich aber häufig ein Reiben der Nackenregion (Regio nuchalis) an Baumstämmen, Ästen, Steinen, Wassertrögen und dergleichen. Dabei senkten die Tiere den Kopf und drückten den Nackenbereich an eine markante Stelle dieser Objekte (Abb. 1) oder ergriffen, aufrecht stehend, mit einer Vorderpfote einen dünnen Zweig und



Abb. 1. Typische Stellung von Krabbenwaschbären (*Procyon cancrivorus*) beim Markieren mit der Nackenregion.

Tabelle 1. Vergleichende Messungen an Hautstrukturen zweier Körperregionen des Krabbenwaschbären.

	Dorsalregion	Nacken
Hautdicke [mm] (Epidermis, Dermis)	2,8 (± 0,1)	4,1 (± 0,4)
Zentrales Primärhaar -		
Länge [mm]	24,7 (± 2,8)	16,8 (± 1,8)
Dicke [µm] -Spitze	10,5 (± 4,6)	12,6 (± 2,9)
Mitte	95,7 (±31,2)	101,9 (± 19,3)
Basis	72,7 (± 19,2)	68,1 (± 15,2)
Zentraler Primärhaarfollikel -		
Länge [mm]	2,8 (± 0,2)	3,3 (± 0,1)
Einsenktiefe [mm]	2,3 (± 0,1)	3,2 (± 0,2)
Dicke [µm]	163 (± 26)	150 (± 23)
Talgdrüsen-Komplex -		
Länge [µm]	446 (± 100)	989 (± 253)
größter Durchmesser [µm]	129 (± 30)	281 (± 69)
Apokriner Schlauchdrüsen-Komplex -		
Länge [mm]	1,2 (± 0,6)	2,4 (± 0,3)
Durchmesser-Endstück [µm]	116 (± 22)	111 (± 18)
Epithelhöhe-Endstück [µm]	26 (± 3,7)	34 (± 3,8)

preßten diesen an den Nacken. Durch kreisende oder vertikale Bewegungen des Kopfes wurde dann die Nackenregion am Gegenstand gerieben. Dieses Verhalten zeigten Krabbenwaschbären beider Geschlechter über den gesamten jahreszeitlichen Verlauf. Es hatte im Vergleich mit den anderen Markierungsaktivitäten einen durchschnittlichen Anteil von 17%. Gemeinsam in einem Gehege gehaltene Tiere überprüften gegenseitig die durch Nackenreiben markierten Stellen und kontrollierten neben der Analregion ab und an auch die Nackenregion des Artgenossen olfaktorisch.

Die genaue Betrachtung der Nackenregion zeigte, daß die Haare in diesem Bereich, entgegen dem normalen Verlauf des Haarstrichs, vom Nacken bis zu den Ohren kopf-

wärts gerichtet waren (Abb. 2). Darüber hinaus wiesen Nackenhaut und basale Anteile der Haare meist einen fettigen, bräunlichen Belag auf, von dem ein intensiver Geruch ausging. Gegenstände oder Teile von Objekten, die von den Krabbenwaschbären mehrmals durch Nackenreiben markiert wurden, waren gleichfalls mit diesem bräunlichen Sekret sowie dem typischen Geruch behaftet.

Die histologische Analyse machte offenkundig, auf welcher strukturellen Basis sich die Produktion des Markierungssekrets im Integument gestaltete. Sehr deutlich und si-

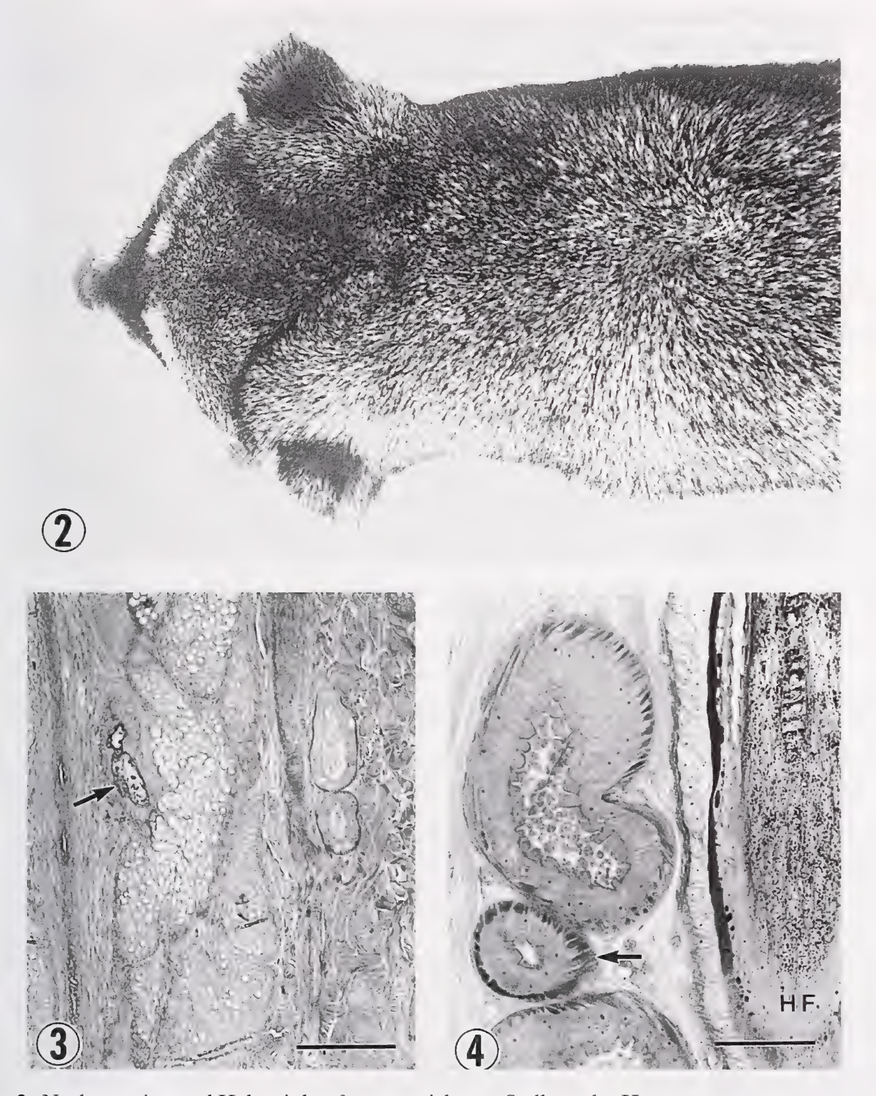


Abb. 2. Nackenregion und Hals mit kopfwärts gerichteter Stellung der Haare.

Abb. 3. Übersicht einer großen Talgdrüse der Nackenhaut mit einem zusätzlichen, oberhalb des Ausführungsganges (Pfeil) gelegenen Anteil (H.E. Färbung, Maßstab entspricht 200 μm).

Abb. 4. Sekretorisches Endstück einer apokrinen Schlauchdrüse der Nackenhaut, mit stark entwickelten Myoepithelzellen (Pfeil), neben einem Haarfollikel (HF) (H.E. Färbung, Maßstab entspricht 50 μm).

gnifkant waren dabei speziell die Unterschiede (Tab. 1) in der Größe bzw. Dicke und Länge der beteiligten Strukturen des Haarfollikelkomplexes im Vergleich der Nackenregion mit der als Kontrolle verwendeten gesamten Rückenregion (hier finden sich bei Säugetieren in der Regel die größten Hautdrüsen der allgemeinen Körperdecke, vgl. z. B. Sokolov 1982; Meyer 1986, 1998; Schwarz und Meyer 1994). Zum ersten zeigte sich die Nackenhaut (Epidermis und Dermis) signifikant ($p < 0{,}01$) als fast doppelt so dick wie die Rückenhaut; zum zweiten offenbarten nicht alle Typen der Haarfollikel, sondern nur die zentralen Primärhaarfollikel und ihre Anhangsdrüsen signifikante Unterschiede ($p < 0{,}01$) zwischen beiden untersuchten Körperanteilen. Außerdem kamen im Nacken zwar keine dickeren, so doch kürzere Haare (Telogen- und ausgewachsene Anagenhaare) als am Rücken vor. Und dies, obwohl die dazugehörigen zentralen Primärhaarfollikel beinahe die doppelte Länge aufwiesen. Besonders auffällig waren die Meßergebnisse von den Anhangsdrüsen, wobei sich im Integument des Nackens mächtige Talgdrüsen entwickelt hatten (Abb. 3), die mehr als doppelt so lang und dick wie an dem entsprechenden Haarfollikeltyp des Rückens hervortraten. Der gesamte sekretorische Anteil der jedem Primärhaarfollikel zugehörigen apokrinen Schlauchdrüse war am Nacken ebenfalls gut doppelt so lang wie am Rücken. Die spezifische histologische Struktur des sekretorischen Endstücks blieb dagegen im Durchmesser des gesamten Endstücks wie in der Epithelhöhe unverändert. Auffallend waren aber die im Nackenbereich immer sehr kräftig ausgebildeten Myoepithelzellen der apokrinen Schlauchdrüsen (Abb. 4).

Diskussion

Die hier vorgelegten Befunde zum Nackenreiben und zur Struktur der Nackenhaut und ihrer Haarfollikelanhangsdrüsen weisen eindeutig auf die spezielle Funktion der Nackenregion des Krabbenwaschbären als Drüsenorgan hin. In diesem Zusammenhang muß keine besonders auffällige strukturelle Veränderung des Integuments vorausgesetzt werden. Eine erhebliche Zunahme der Größe bzw. Volumina der Anhangsdrüsen von Primärhaarfollikeln bei fehlender relativer Größenzunahme des Haarfollikels selbst ist z. B. sehr klar im Integument der Anogenitalregion des Pferdes erkennbar (Tsukise und Meyer 1987; Meyer 1998) oder in der Skrotalhaut des Makaken (*Macaca cyclopis*) (Meyer und Tsukise 1989). Auch das Reiben der Hals- und Nackenregion an Bäumen und Gebüsch, wie zur Territorialmarkierung beim Reh (*Capreolus capreolus*) beobachtet, konnte nicht mit außerordentlichen Abwandlungen der Hautstruktur dieser Körperteile korreliert werden (Sokolov 1982). Nackendrüsen, die fettige, duftende Flüssigkeiten sezernieren und durch Haarbüschel gekennzeichnet sind, scheinen jedoch bei Fledermäusen (spez. Pteropodidae) vorzuliegen, obwohl eine histologische Verifizierung des Drüsenorgancharakters unseres Wissens nach noch fehlt (Schaffer 1940; Quay 1970). Als Sonderfall seien vergrößerte apokrine Schlauchdrüsen in der Nackenregion junger nordamerikanischer Nerze (*Mustela vison*) erwähnt, die allerdings nur in der Saugperiode vorhanden sind und danach angeblich degenerieren. Eventuell helfen diese Drüsen der Mutter, ihre Nachkommen besser olfaktorisch zu differenzieren (Yager et al. 1988).

Von entscheidender Wichtigkeit ist im vorliegenden Fall eine – wie bei typischen Drüsenorganen – regional und zeitlich separat anzusteuernde Aktivität der Anhangsdrüsen der großen Primärhaarfollikel zur Produktion einer großen Menge an guthaftendem, fettreichem Sekret, dessen bakterielle Zersetzung ein offenbar individual spezifisches Duftmuster hervorbringt. Dies gilt im besonderen unter der oben beschriebenen Beobachtung, daß nicht nur die markierten Objekte olfaktorisch überprüft wurden, sondern gelegentlich die Nackenregion der jeweiligen Gruppenmitglieder miteinbezogen war. Das typische Verhaltensmuster des Nackenreibens an Gegenständen ist von Kampmann

(1972) und LÖHMER (1973) auch bei in Gehegehaltung lebenden nordamerikanischen Waschbären gefunden worden. Diesen Autoren zufolge trat es bei *Procyon lotor* allerdings vornehmlich während der Fortpflanzungsperiode der Tiere auf und wurde vor allem von männlichen Waschbären ausgeführt. Beim nordamerikanischen Waschbären zeigt sich – im Unterschied zum Krabbenwaschbär – im Bereich des Nackens zudem keine dem normalen Haarstrich entgegenlaufende Ausrichtung der Haare. Welche spezielle biologische Bedeutung das beim Krabbenwaschbären sehr ausgeprägte Markieren mit Hilfe der Nackenregion wirklich hat, kann nur vermutet werden. Eventuell deutet es auf ein stärker ausgeprägtes Territorialverhalten als bei *Procyon lotor* hin. Unterstützt wird diese Annahme durch die beobachtete höhere innerartliche Aggressionsbereitschaft der Krabbenwaschbären. Desweiteren besteht die Möglichkeit, daß die mit einem individualspezifischen Geruch behaftete Nackenregion eine Rolle bei der Auswahl des Sexualpartners spielt.

Danksagung

Wir danken Frau CLAUDIA BÖDEKER und Frau INES BLUME für ihre wertvolle technische Assistenz.

Zusammenfassung

Die Arbeit beschreibt zum ersten Mal das Reiben der Nackenregion an Gegenständen als regelmäßige und häufig angewendete territoriale Markierungsweise bei im Gehege gehaltenen Krabbenwaschbären (*Procyon cancrivorus nigripes*). Der Nacken der Tiere wies eine entgegen dem normalen Haarstrich verlaufende Ausrichtung der Haare auf. Die mittels typischer kreisender oder vertikaler Kopfbewegungen mit einem fettigen und duftenden Sekret markierten Objekte wurden von Artgenossen olfaktorisch kontrolliert. Eine histologische Analyse des Integuments der Nackenregion zeigte im Vergleich zum gesamten Rückenbereich eine dickere Cutis und erheblich größere Komplexe der Talgdrüsen und apokrinen Schlauchdrüsen von zentralen Primärhaarfollikeln, die in Dicke und Länge allerdings denjenigen im Rückenbereich entsprachen. Die mögliche biologische Bedeutung dieses „Nackendrüsenorgans" beim Krabbenwaschbär wird diskutiert.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Daylight behaviour of Humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa

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Receipt of Ms. 17. 12. 1997
Acceptance of Ms. 19. 08. 1998

Abstract

Data on the daylight behaviour of humpback dolphins *Sousa chinensis* were collected during sea- and land-based surveys undertaken in Algoa Bay, Eastern Cape, South Africa, throughout a three year period. Dolphin activities/behaviour were categorised as: "feeding", "travelling", "opportunistic feeding", "socialising and playing", "resting" and "other". It seems apparent that behaviour determines the spatial geometry of the dolphin group, but not the group size. The surfacing-breathing interval is similar for "feeding", "opportunistic feeding", and slow "travelling", but differs considerably from the pattern displayed during fast "travelling". Daylight behaviour of humpback dolphins is dominated by "feeding" and shows a regular pattern which is probably governed by the diurnal cycles of their prey. Generally, "feeding" peaks in the morning and gradually decreases through the rest of the day. As "feeding" decreases, "travelling" and "opportunistic feeding" increase, both peaking in the afternoon. "Resting" and "socialising and playing" occur with similar frequency throughout the day. This pattern varies little between summer and winter, as does the overall proportion of daylight behaviours. The only significant seasonal difference is in the frequency of "social/sexual" behaviour which peaks in summer. Although tidal cycle influences to some extent the behaviour of humpback dolphins, in Algoa Bay their daylight activity/behaviour is predominantly governed by time of day.

Key words: *Sousa chinensis*, daylight behaviour pattern, seasonal variation.

Introduction

Activity rhythms of animals represent an adaptation to seasonal and diurnal variations of environmental factors and are a result of a complex compromise between optimal foraging/feeding time, social activities, and environmental constraints (CLOUDSLEY-THOMPSON 1961; NIELSEN 1983). Diurnal and seasonal patterns of activity and behaviour have been described in detail for several terrestrial mammals. There is, however, a disproportionate lack of similar information concerning cetaceans (for review see KLINOWSKA 1986; SHANE et al. 1986). One reason for this lies in the practical difficulty of studying the behaviour of free-ranging cetaceans.

Humpback dolphins *Sousa chinensis* inhabit Indo-Pacific coastal waters and are known to occur along the east and south coast of South Africa (ROSS et al. 1994). Despite its inshore occurrence, there has been little study of this species and much of our knowledge is based on fragmentary information. Only recently has the natural history of humpback dolphins been investigated in detail in the Algoa Bay region on the south Eastern Cape coast of South Africa (KARCZMARSKI 1996). This long term study, although

0044-3468/99/64/01 – 019 $ 12.00/0

not strictly behavioural in its design, included many hours of observations and provided a good opportunity to collect observational data on dolphin behaviour. It was possible to quantify the daylight activity pattern of humpback dolphins and examine the daytime, seasonal, and tidal variations in their behaviour. Not only are these observations important in themselves, but they provide a valuable insight into the daily lives of this coastal dolphin. Furthermore, a better understanding of the ecological determinants of humpback dolphin behaviour may help in the development of appropriate protective measures for this little known and apparently threatened (Klinowska 1991) species.

Material and methods

Algoa Bay is the easternmost and largest of several shallow (mean depth < 50 m), log spiral bays found on the south-east coast of South Africa (Fig. 1). The Bay, flanked on the western side by Cape Recife (34°02′ S; 25°42′ E) and on the eastern side by the less prominent Cape Padrone (33°46′ S; 26°28′ E), is located along a generally exposed coastline and represents an open habitat with few surface geographical boundaries.

The behaviour of humpback dolphins was recorded during land- and sea-based surveys undertaken in the south-western part of Algoa Bay between May 1991 and May 1994. Daily land-based surveys usually started 1–2.5 hours after sunrise (weather permitting) and observations of the inshore waters, to approximately 1 km offshore, were carried out from several visually overlapping vantage points. Sea-based surveys were opportunistic, limited by both the presence of dolphins and weather conditions and were conducted using a 3.5 m inflatable boat powered by a 30 HP outboard engine.

The activity/behaviour of the focal group of dolphins (sensu Altmann 1974) was usually recorded at the commencement of each sighting and, thereafter, randomly for five minute intervals throughout the survey. For each of the five minute intervals, the lenght of time spent in different behaviours (see below) was estimated in the form of percentage. The raw field data were subsequently grouped into hourly intervals according to the time of day and into four tidal periods (1/2 low, low, 1/2 high, high) in which they were collected. During boat surveys, recording of dolphin behaviour began only after the animals were assumed to have become habituated to the presence of the boat – in most cases at least 30 minutes from the initial sighting and with the boat at a distance of 10–20 meters from the group. It was assumed that this gave the animals time to resume their normal activity (see also Acevedo 1991; Ballance 1992).

Generally, because aggregations of humpback dolphins were small (mean = 7 dolphins, sd = 2.52; Karczmarski 1996; Karczmarski et al. 1998) the whole group was often the focus of observations and it was possible to categorise the behaviour of the group as a whole (the predominant activity of the majority of the group members). Six broad categories of behaviour were distinguished:

The first category consisted of frequent and asynchronous dives, in varying directions, in one location, with an evident lack of directional movement; surfacing and respiration displayed no obvious pattern. During this activity dolphins often chased fish and occasionally fish capture was seen. Consequently, it is likely that this complex of behaviours represents feeding and is therefore referred to as "feeding".

The second category was characterised by persistent, directional movement, with all group members diving and surfacing synchronously. Chasing of fish or even social behaviour was extremely uncommon during this behaviour and, consequently, it is referred to as "travelling".

The third category appeared to be a combination of the previous two. Dolphins moved slowly, but usually in a fairly consistent direction. However, surfacing and diving were apparently less synchronised than during apparent "travelling". Furthermore, the directional movement was frequently interrupted by short bouts of localised movement (frequent changes in direction with no evident overall direction), during which some individuals performed long dives. Occasionally chasing of fish was seen. Social activity during this behaviour was uncommon. It was assumed that this pattern of activity represented "opportunistic feeding" and it is referred to as such.

The fourth category consisted of various vigorous activities including leaping out of the water, riding waves in the surf zone, high speed movement with frequent direction changes, and prolonged body contact with other dolphins. These were frequently accompanied by prolonged bouts of almost constant physical contact between two or more dolphins, which seemed to have a sexual meaning (see also

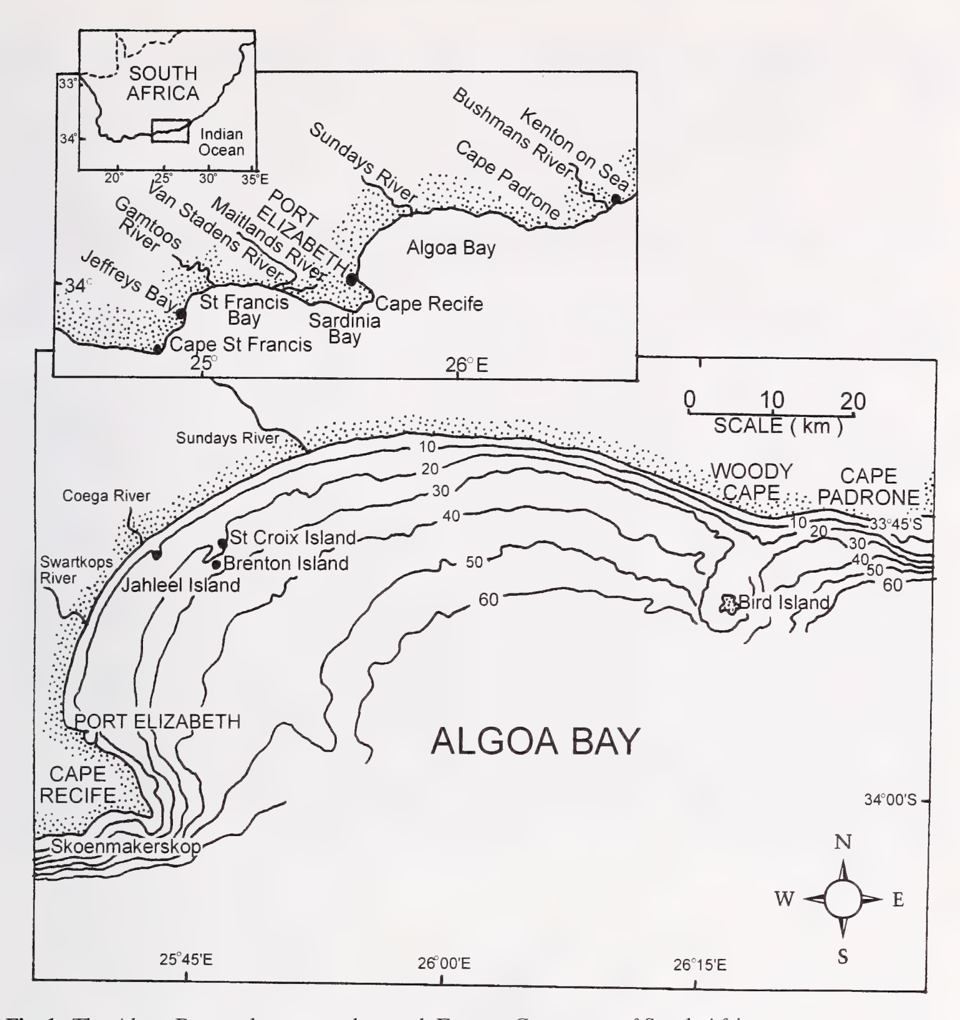


Fig. 1. The Algoa Bay study area on the south Eastern Cape coast of South Africa.

Karczmarski et al. 1997). It seems most likely that these activities served a social function and are referred to as "socialising and playing".

The fifth category consisted of a low level of activity, with the dolphins apparently floating stationary and motionless at the surface, with some occasional slow forward movement. This is referred to as "resting".

Activities which could not be easily assigned to any of the above categories were termed "other".

No underwater observations were conducted and dolphin behaviour is described as it was observed from the research boat. The spatial geometry of the dolphin group (after Shane 1990 a), its size, composition, and locality were noted at the commencement of each sighting and when any variable changed.

Two seasons. summer and winter, are distinguished here. "Summer" is defined as the period when the mean temperature of the inshore surface water is higher than the annual mean (18 °C). The period when the surface water temperature drops below this annual mean is referred to as "winter". In general, the first days of May mark the beginning of "winter" and late October marks the beginning of "summer".

The term "group" refers to any aggregation of more than one dolphin, including all age classes, within visual range of the survey team. Typically, these animals were in apparent association and en-

gaged in similar activities for most of the observation period. Each time a group was observed, it was recorded as a "sighting". The term "sighting", however, has a wider meaning and includes solitary animals.

Results

Groups and solitary humpback dolphins were observed 104 times during more than 300 hours of observations. Dolphin behaviour was specifically recorded for a minimum of one hour during 83 sightings, for a total of 270 hours. In most instances, behaviour was recorded for between three and four hours (mean = 3.2 h), though the longest session exceeded six hours.

Groups of humpback dolphins varied in size from three to 24 animals with a mean of seven (sd = 2.52). Solitary individuals were seen frequently and constituted 15.4 % (n = 16) of sightings (see also Karczmarski et al. 1998). In most cases the size of groups remained unchanged throughout observations and was not affected by the animals' behaviour (Kruskal – Wallis ANOVA, KW = 39.57, n = 361, p = 0.53). Group geometry, however, was not random but varied according to activity. During "feeding", the dolphins were usually widely dispersed, with the distances between individuals varying constantly and ranging between approximately 1 m and at least 100 m. When "travelling", humpback dolphins formed a tight "single-file group", or fairly compact, oval shaped aggregation with the distance between individuals seldom exceeding a body-length of an adult dolphin (circa 2.5 m). The position of individuals within such groups, however, changed continually. During "opportunistic feeding" group geometry was not well defined, with dolphins moving in the same direction, but in a fairly dispersed aggregation; less dispersed, however, than during "feeding" (the max. distance between individuals usually < 50 m). Similarly, humpback dolphins did not display any consistent group geometry during "socialising and playing" or "resting". The distances between individuals changed continually, ranging between a "touching distance" when body contact was performed and circa 25 m.

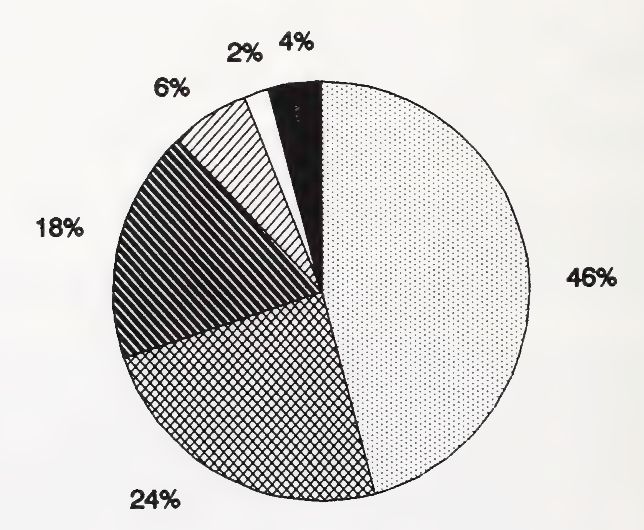


Fig. 2. The mean proportion (%) of daylight hours spent by humpback dolphins in each of six behaviours (▒ – feeding, ▒ – travelling, ▒ – opportunistic feeding, ▒ – socialising and playing, ☐ – resting and ■ – other) in Algoa Bay between May 1991 and May 1994.

The surfacing-breathing interval did not vary significantly between "feeding" (mean = 25.6 sec., n = 36, sd = 17.3), "opportunistic feeding" (mean = 30.1 sec., n = 27, sd = 11.8) and slow "travelling" (mean = 23.3 sec., n = 29, sd = 7.1); (Kruskal – Wallis ANOVA, KW = 17.44, n = 92, p = 0.61). During these behaviours humpback dolphins ventilated by rolling at the surface with an overall mean interval of 26.3 sec. (sd = 12.7). This pattern changed considerably during fast "travelling" (n = 27), when several (4 to 9, mean = 6, sd = 1.7) rapid ventilations separated by only a few seconds (mean = 8.6 sec., sd = 4.1) alternated with a long submergence of mean duration = 101.3 sec. (sd = 20.9), during which a long distance was travelled at high speed.

The daylight activity of humpback dolphins in Algoa Bay was dominated by "feeding" (Fig. 2). Behaviours classified as "feeding" and "opportunistic feeding", if combined, contributed well over 50 % of all recorded activities. "Travelling" represented the second most frequently seen behaviour, while "resting" or "socialising and playing" were infrequent and accounted for less than 10 % of the dolphins' daylight activities.

Humpback dolphins in Algoa Bay displayed little seasonal difference in the proportion of diurnal behaviours (Fig. 3). Although dolphins appeared to spend more time "feeding" in winter and, inversely, less time on "opportunistic feeding", none of these differences were significant (Mann-Whitney, U = 87.50, n = 83, p = 0.38 and U = 95.00, n = 83, p = 0.20, respectively). The proportion of combined "feeding" and "opportunistic feeding" was similar for both summer (63.0 %) and winter (64.3 %). The only signifcant seasonal difference was for "socialising and playing" (Mann-Whitney, U = 105.00, n = 83, p = 0.05) (Fig. 3). The summer frequency of "socialising and playing" was double that of winter. The sexual component of this behaviour was also significantly greater in summer (47.2 %) than in winter (11.3 %) (Mann-Whitney, U = 240.00, n = 65, p < 0.0001).

The proportion of daylight hours spent in different behaviours was well defined and varied significantly throughout the day (Fig. 4) for both summer (Kruskal – Wallis ANOVA, n = 181, KW = 57.08, p < 0.0001 for "feeding": KW = 56.72, p < 0.0001 for "travelling"; KW = 25.89, p = 0.007 for "opportunistic feeding"; KW = 35.69, p = 0.0002 for "so-

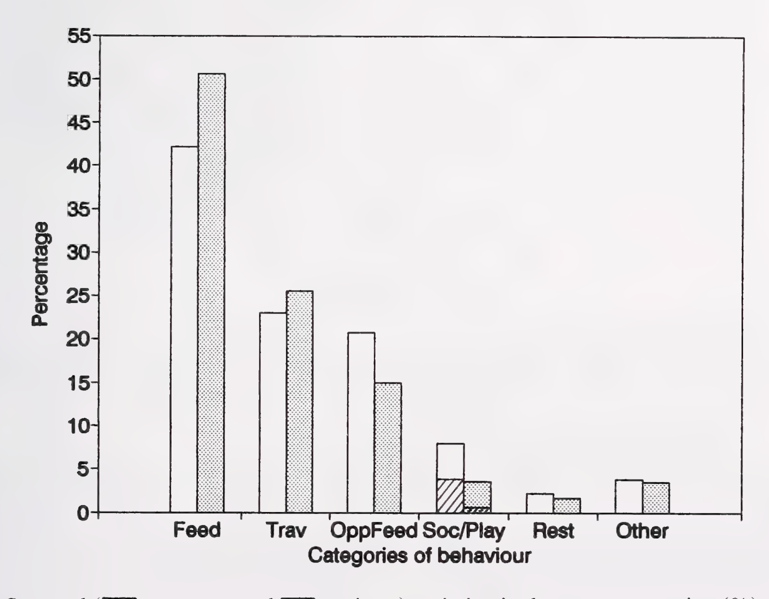


Fig. 3. Seasonal (☐ – summer and ▒ – winter) variation in the mean proportion (%) of diurnal behaviours displayed by humpback dolphins in Algoa Bay between May 1991 and May 1994. Sexual behaviour (▨) as a proportion (%) of socialising and playing is also shown.

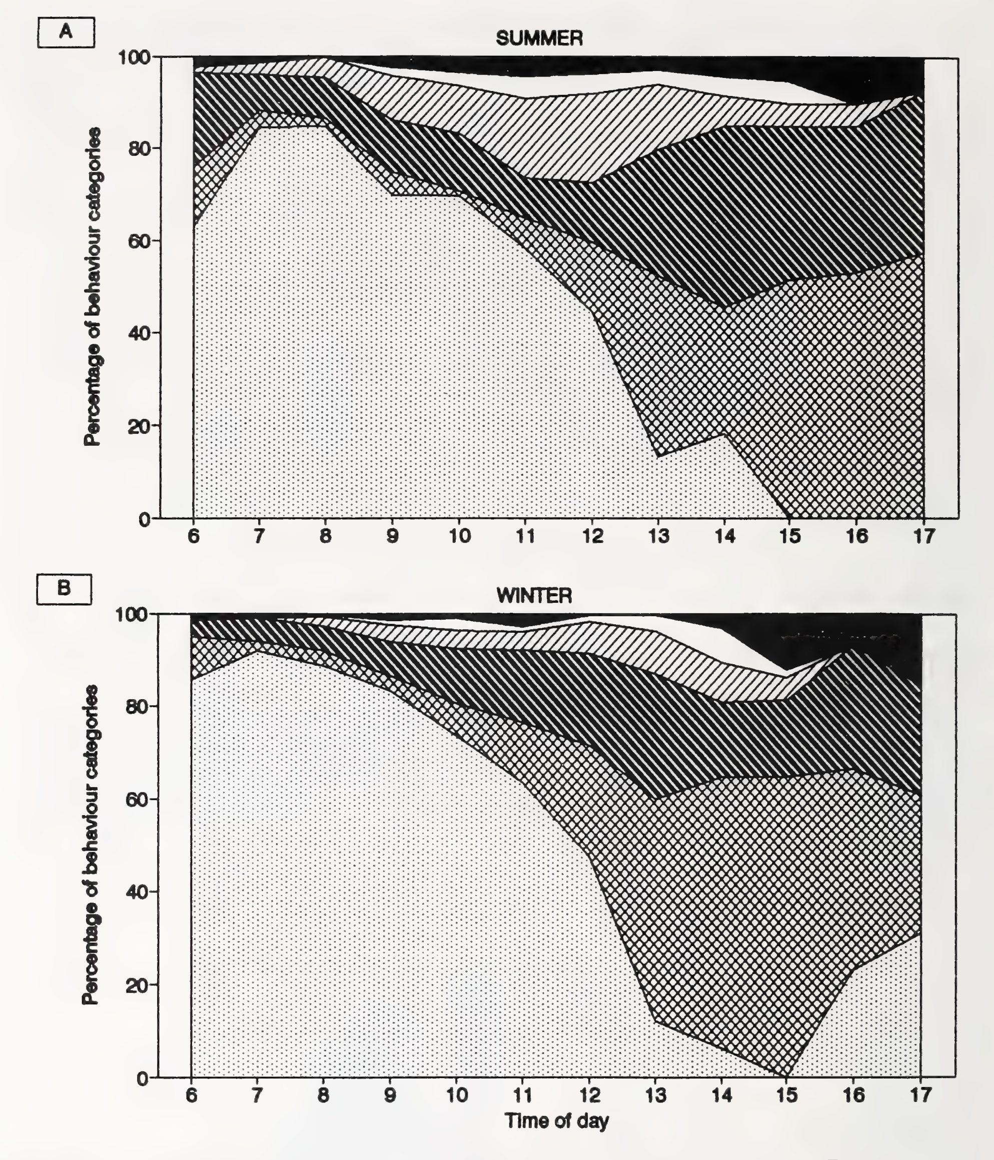


Fig. 4. The mean hourly proportion (%) of the diurnal behaviours (▒ – feeding, ▒ – travelling, ▒ – opportunistic feeding, ▒ – socialising and playing, □ – resting and ■ – other) of humpback dolphins observed in Algoa Bay between May 1991 and May 1994 for both summer (A) and winter (B).

cialising and playing" and KW = 31.87, p = 0.0008 for "resting") and winter (Kruskal – Wallis ANOVA, n = 102, KW = 62.15, p < 0.0001 for "feeding"; KW = 59.20, p < 0.0001 for "travelling"; KW = 27.96, p = 0.003 for "opportunistic feeding"; KW = 33.21, p = 0.0005 for "socialising and playing" and KW = 24.31, p = 0.01 for "resting"). Generally, "feeding" peaked in the morning and gradually decreased through the rest of the day. As "feeding" decreased, "travelling" and "opportunistic feeding" increased, both peaking in the afternoon. During winter evenings the frequency of "travelling" and "opportunistic feeding" decreased again, with a corresponding secondary increase in "feed-

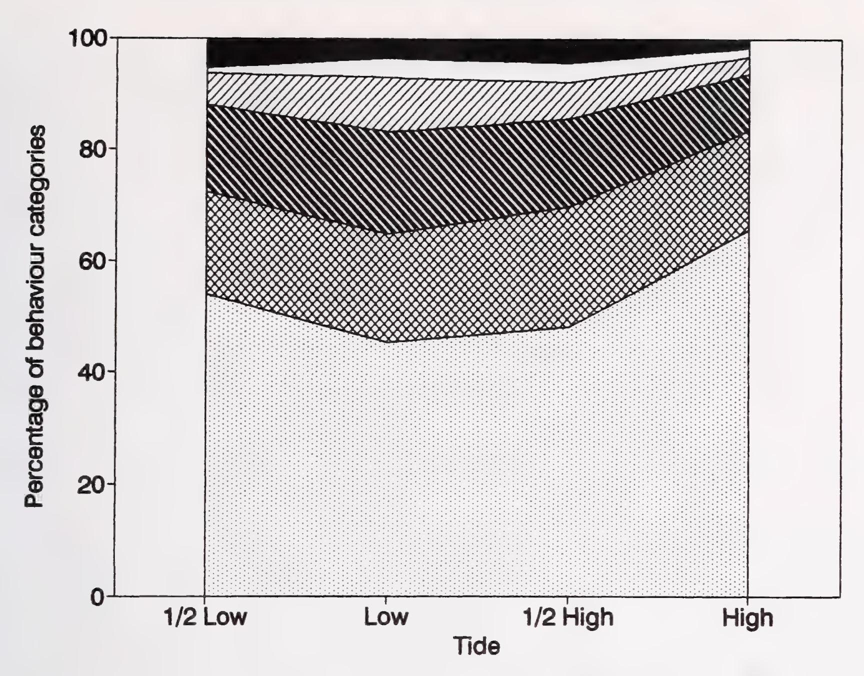


Fig. 5. Tidal influence on the diurnal behaviours ([dotted box] – feeding, [cross-hatched box] – travelling, [dark hatched box] – opportunistic feeding, [hatched box] – socialising and playing, [empty box] – resting and [black box] – other) of humpback dolphins in Algoa Bay observed between May 1991 and May 1994.

ing". Prolonged bouts of "resting" and "socialising and playing" occurred with similar frequency throughout the day, but were slightly less evident in the morning and evening. There was, however, a clear summer increase in "socialising and playing" behaviour around midday.

The behaviour of humpback dolphins in Algoa Bay did not appear to be significantly related to the tides (Fig. 5), except for "feeding" which increased during high tide (Kruskal – Wallis ANOVA, KW = 27.85, n = 102, p = 0.05).

Discussion

The six categories of behaviour distinguished in the present study are generally consistent with the types of behaviour observed and classified in several other studies (Saayman and Tayler 1979; Shane 1990 a, b; Ballance 1992; Brager 1993). Behaviour of humpback dolphins in Algoa Bay appeared to determine the spatial geometry of the group in a similar way as has been observed for other cetaceans (Shane 1990 a; 1995) which suggests a functional significance. The tight structure of a "travelling" group may possibly reduce the likelihood of incidental separation of an individual from the group, increase the sensory invigilation of the area being travelled through and possibly (as observed by Saayman and Tayler 1979) facilitate an active, co-operative defence. Furthermore, because swimming at the surface seems to require 4.5 times more energy than swimming at a depth of about one-half of body length (Au and Weihs 1980; Hui 1987) the long distance covered underwater during fast "travelling" is likely to be energetically beneficial (Hui 1989).

The close proximity of group members during "resting" could possibly increase safety of an individual due to sensory integration of a group (e. g. Norris and Dohl 1980 a). The

dispersed geometry of groups engaged in "feeding" and "opportunistic feeding" on the other hand, appears to be related to the foraging/feeding behaviour used by the animals (Würsig 1986). The widely dispersed "feeding" groups indicate that individual, rather than co-operative, feeding is likely to be the norm for humpback dolphins in Algoa Bay.

Feeding dominated the daylight activity of humpback dolphins in Algoa Bay, as has also been observed for bottlenose dolphins in the bay system of Galveston, Texas (Brager 1993). However, the overall proportions of daylight behaviours recorded for humpback dolphins during the present study vary considerably from those described by Saayman and Tayler (1979) for humpback dolphins in Plettenberg Bay. The proportions of time dolphins were seen feeding (26.5 %) and travelling (50 %) in Plettenberg Bay are almost the reverse of those in Algoa Bay. One reason for this could be that, despite an apparently similar definition of behaviour categories, the actual classification of behaviour observed in the field differed considerably between the two studies. Alternatively, it is possible that there are several other factors which differ between Algoa Bay and Plettenberg Bay.

The time spent on non-feeding behaviours appears to be proportional to feeding efficiency (Herbers 1981). As feeding efficiency increases, less time is spent searching for or capturing prey and more time is available for less active behaviour. Feeding efficiency is likely to increase with richness of habitat and, inversely, more time is likely to be required for feeding where food is not so plentiful. Consequently, the overall proportion of diurnal behaviours is likely to be a function of the habitat and biological needs of the animals and the considerably smaller proportion of daylight hours occupied by feeding in Plettenberg Bay may reflect a greater abundance of the inshore prey resources.

Furthermore, as discussed in Karczmarski (1996), the Plettenberg Bay region houses a multitude of shallow rocky reefs which facilitate feeding for humpback dolphins. In contrast, only the south-westerly bight of Algoa Bay has abundant shallow reefs. Consequently, it is possible that humpback dolphins use the areas of Algoa Bay and Plettenberg Bay differently, with several feeding sites in the Plettenberg Bay region; but apparently only one (limited in size) primary feeding ground in Algoa Bay, where feeding is particularly intensive. By comparison, the overall proportion of daylight behaviours observed for bottlenose dolphins *Tursiops truncatus* on their estuarine feeding grounds in the Gulf of California, Mexico (Ballance 1992) is strikingly similar to that of humpback dolphins in Algoa Bay. On the other hand, the proportion of time humpback dolphins spent feeding and travelling in Plettenberg Bay is strikingly similar to that reported by Ballance (1992) for bottlenose dolphins when the animals were away from their estuarine feeding grounds.

Humpback dolphins in Algoa Bay displayed little seasonal difference in the overall proportion/frequency of daylight behaviours. Only "social" and "sexual" behaviour showed a seasonal difference, increasing in summer. This corresponds with the summer peak of calving observed for humpback dolphins in Algoa Bay (Karczmarski 1996) and, consequently, supports the one year gestation period suggested for this species (V. G. Cockcroft, unpubl. data). Similarly, a seasonal (spring and summer) increase in social behaviour, as well as abundance of calves, was observed for bottlenose dolphins off the Texas coast (Shane 1990 b).

The general lack of seasonal variation in the overall frequency of other behaviours – particularly feeding – is surprising, considering possible changes in energy requirements of the dolphins due to declining water temperature (Cockcroft and Ross 1990; Ross and Cockcroft 1990). There was, however, an apparent increase in feeding behaviour during winter evenings in Algoa Bay, which may possibly reflect an increased energetic demand of the dolphins or, alternatively, an increase in prey abundance on winter evenings Because of early nightfall in winter, all evening observations were discontinued between 17h00 and 18h00 (compared to 19h00–20h00 in summer). In winter, however, the second-

ary feeding peak increased at this time, while no feeding was observed during evenings in summer. Consequently, it is possible that in winter feeding occupies a larger proportion of humpback dolphin activity than was apparent during the present study.

The proportion of daylight which humpback dolphins used for different behaviours varied considerably throughout the day and formed a distinct diurnal pattern. This pattern seems to follow the solar day and is, possibly, to a large degree shaped by the diurnal cycles of the prey species. A similar phenomenon is apparent for several populations of coastal bottlenose dolphins (Saayman et al. 1973; Würsig and Würsig 1979; Shane 1990 b; Brager 1993; Hanson and Defran 1993), as well as other cetacean species (e. g. Norris and Dohl 1980 b; Würsig and Würsig 1980; Klinowska 1986). Data on the diurnal variability in abundance, density or distribution of the inshore prey resources in Algoa Bay are, however, scarce. The only reported fluctuation in the biomass of fish in the surf zone of Algoa Bay is thought to be related to the tidal cycle and increases during low tide; while the species diversity apparently increases just after twilight (Lasiak 1982, 1984). A better understanding of the diurnal cycles of the inshore fish and squid species in Algoa Bay could contribute substantially to our understanding of humpback dolphin diurnal activity/behaviour patterns.

Feeding was the only behaviour of humpback dolphins apparently affected by the tides in Algoa Bay. However, the increase in feeding during high tide in Algoa Bay was less evident than that reported by Saayman and Tayler (1979) in Plettenberg Bay. Saayman and Tayler (1979) speculated that an apparent increase in shoaling behaviour of some reef associated prey species during high tide could increase their "relative accessibility" for dolphins and consequently shape the entire daylight activity pattern of humpback dolphins. This appears less so in Algoa Bay where the biomass of fish in the surf zone is reported to increase at low tide (Lasiak 1982, 1984).

Several other studies conducted in a number of coastal habitats showed various degrees of influence of the tidal cycle on dolphin movement and activity (e. g. Würsig and Würsig 1979; Shane 1990 b: Hanson and Defran 1993; Felix 1994). It seems apparent that the influence of tides, although relatively strong in enclosed bays, passes and narrow channels, generally decreases with the openness of habitat. As the Algoa Bay region is a part of an exposed coastline where wave energy is considerably greater than tidal energy, a limited tidal impact on dolphin activity/behaviour could be expected.

Overall, humpback dolphin behaviour appears similar to that described for other coastal dolphin species like the bottlenose dolphin. The present study, however, was not designed to be strictly behavioural; data on dolphin behaviour were collected opportunistically, as part of a larger scale research project. Consequently, a clear understanding of the behaviours of humpback dolphins and the relevance of these to the fulfilment of their biological and social needs requires further investigation.

Acknowledgements

This work would not have been possible without the financial assistance of the Foundation for Research Development (FRD), WWF South Africa and the University of Port Elizabeth, which is gratefully acknowledged. We wish to express our thanks to Meredith Thornton, Jimmy Henderson, and Shane Norris for their help during fieldwork. We thank Randall Wells (Dolphin Biology Research Institute, Mote Marine Laboratory, Sarasota, Florida, USA), Bernd Würsig (Texas A & M University at Galveston, USA), Anton McLachlan and Deo Winter (University of Port Elizabeth, South Africa) and anonymous reviewers for their comments on the earlier draft of the manuscript; and Nina Wozniak (German Department, University of Port Elizabeth) for her help with translation of Zusammenfassung.

Zusammenfassung

Tagesgang im Verhalten von Buckeldelphinen Sousa chinensis in Algoa Bay, Südafrika

Daten zum Tagesverhalten von Buckeldelphinen *Sousa chinensis* wurden über einen Zeitraum von drei Jahren in der Algoa-Bucht, Ostkapprovinz, Südafrika, in Aufnahmen auf See und vom Land aus erstellt. Die Aktivitäten und Verhaltensweisen der Delphine wurden eingeteilt in: „Nahrungsaufnahme", „Fortbewegung", „opportunistische Nahrungsaufnahme", „gesellschaftliches Verhalten und Spiel", „Ausruhen" und „Anderes". Das Verhalten der Buckeldelphine bestimmt die räumliche Geometrie der Delphingruppe, nicht aber die Gruppengröße. Die Intervalle des Einatmens an der Wasseroberfläche sind ähnlich bei „Nahrungsaufnahme", „opportunistischer Nahrungsaufnahme" und bei langsamer „Fortbewegung", weichen jedoch stark von dem Verhaltensmuster bei schneller „Fortbewegung" ab. Das Tagesverhalten des Buckeldelphins wird von der „Nahrungsaufnahme" dominiert und weist eine starke Regelmäßigkeit auf, die wahrscheinlich von den Tageszyklen der Beutetiere gesteuert wird. Allgemein hat die „Nahrungsaufnahme" morgens ihren Höhepunkt und nimmt im Laufe des Tages allmählich ab. Während die „Nahrungsaufnahme" abnimmt, nehmen „Fortbewegung" und „opportunistische Nahrungsaufnahme" zu und zeigen am Nachmittag gleichsam Höchstwerte. Die Frequenz der Aktivitäten „Ausruhen" und „gesellschaftliches Verhalten und Spiel" bleibt ganztägig etwa gleich, ist aber morgens und abends etwas geringer. Dieses Verhaltensmuster variiert nur geringfügig zwischen Sommer und Winter, ebenso wie das gesamte Verhältnis der Tagesverhaltensweisen. Der einzige bemerkenswerte Unterschied für die Jahreszeiten ist die Frequenz des „gesellschaftlichen/Paarungsverhaltens", das im Sommer seinen Höhepunkt hat. Daraus scheint hervorzugehen, daß die Gesamtproportion der Tagesverhalten der Delphine von ihrem Habitat und ihren biologischen Bedürfnissen determiniert wird. Obwohl der Gezeitenzyklus das Verhalten der Buckeldelphine in einigem Maße beeinflußt, sind Tagesaktivitäten und -verhalten vornehmlich von der Tageszeit bestimmt. Bei zukünftigen Forschungsaufgaben sollten nächtliches Verhalten wie auch das Verhältnis zwischen verschiedenen Verhaltensformen und potentiellen Störfaktoren berücksichtigt werden.

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Z. Säugetierkunde **64** (1999) 30–35



ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Allozyme variation and taxonomic status of *Calomys hummelincki* (Rodentia, Sigmodontinae)

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Receipt of Ms. 16. 05. 1994
Acceptance of Ms. 12. 10. 1998

Abstract

The level of genetic polymorphism was analyzed in a population sample of *Calomys hummelincki* from Venezuela. Enzymes and proteins studied by means of gel electrophoresis give information on 30 loci. The proportion of polymorphic loci was 40 %, and mean expected heterozygosity (H_e) was 12.7 %. These values are higher than those reported for most species of rodents in the northern hemisphere, but are comparable to those observed in other Sigmodontinae species from Argentina. Nei's genetic distance (D_N) with the species *C. laucha*, *C. venustus*, and *C. musculinus* ranged from 0.289 to 0.494. D_N values between populations of different Sigmodontinae species are below 0.09. A distance Wagner tree based on modified Rogers' distances shows that *C. hummelincki* is more closely related to *C. venustus* than to *C. laucha*. Our data support the proposal that *C. hummelincki* and *C. laucha* are fully distinct species.

Key words: *Calomys hummelincki*, Sigmodontinae, allozymes, polymorphisms

Introduction

Among the Sigmodontinae rodents (family Muridae) of the tribe Phyllotini, the genus *Calomys* shows a wide distribution in South America. The systematics of this genus, as well as the geographic distribution and ecology of some of its species are still poorly known. The taxonomic status of one of these species, *Calomys hummelincki* (Venezuelan pigmy mouse) has been a matter of controversy. The species was first described by Husson (1960) on the basis of specimens collected on islands of the Caribbean sea and included in the genus *Baiomys*. Later, Hershkovitz (1962) reported on this rodent also from Venezuela, assigning it to the genus *Calomys* as synonym of *C. laucha*. In 1976, Handley recognized the species *Calomys hummelincki* as being different from *C. laucha* and described its geographic distribution in the Orinoco plains and the deserts around the Gulf of Venezuela. The first study on karyologic differences between these species was conducted by Perez Zapata et al. (1987), who reported a karyotype of 2n = 60, FN = 64 for *C. hummelincki*, fairly distinct from that of *C. laucha* (2n = 64, FN = 68).

As a contribution to the knowledge of the systematics and evolution of South American murids of the subfamily Sigmodontinae, we present here an analysis of allozymic polymorphism in *Calomys hummelincki* and an estimation of its genetic distance from the species *C. laucha*, *C. venustus*, and *C. musculinus*.

0044-3468/99/64/01 – 030 $ 12.00/0

Material and methods

Seventeen specimens of *C. hummelincki* collected in Planicie Costera de Adícora (11°55′N; 69°49′W) Estado Falcón, Venezuela, were studied. Preparation of tissue homogenates, electrophoretic and staining procedures were carried out as described by Gardenal et al. (1980) and Gardenal and Blanco (1985). The following enzymes were analyzed: soluble esterases (ES-1 to ES-6; E.C. 3.1.1.1), aspartate aminotransferases (AAT-1 and AAT-2; E.C. 2.6.1.1), catalase (CAT; E.C. 1.11.1.6), adenylate kinase (AK; E.C. 2.7.4.3), phosphoglucomutases (PGM-1 and PGM-2; E.C. 2.7.5.1), superoxide dismutases (SOD-1 and SOD-2; E.C. 1.15.1.1), liver acid phosphatase (ACP_L; E.C. 3.1.3.2), kidney acid phosphatase (ACP_K; E.C. 3.1.3.2), malic enzyme (ME; E.C. 1.1.1.40), malate dehydrogenases (MDH-1 and MDH-2, E.C. 1.1.1.37), lactate dehydrogenase (LDH-1 and LDH-2, E.C. 1.1.1.27), NADP-isocitrate dehydrogenases (IDH-1 and IDH-2, E.C. 1.1.1.42), 6-phosphogluconate dehydrogenase (6-PGDH, E.C. 1.1.1.44), glucose-6-phosphate dehydrogenase (G6PDH, E.C. 1.1.1.49), glycerophosphate dehydrogenase (GPDH, E.C. 1.1.1.8), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), and NAD-linked nonspecific dehydrogenase (NDH). In addition, other proteins were studied in serum: transferrin (Tf) haptoglobin (Hpt) and albumin (Alb). Altogether, these proteins give information on genetic variation at 30 loci.

Statistics

Average heterozygosity per individual and proportion of polymorphic loci were estimated from the 30 loci analyzed. Genetic distance (D_N) indices were calculated according to Nei (1972) and Rogers modified by Wright (1978). Calculations were based on the allele frequencies at 20 loci reported previously for comparisons between the species *C. musculinus, C. laucha*, and *C. venustus* (Gardenal et al. 1990). A distance Wagner tree (rooted at midpoit of longest path) was constructed on the basis of modified Rogers' distances (Wright 1978) between the four species. All calculations were performed by using the BIOSYS-1 program (Swofford and Selander 1981).

Results and discussion

Table 1 shows allele frequencies for 12 polymorphic loci in *C. hummelincki*. Expected average heterozygosity (H_e) was 12.7 % and observed average heterozygosity (H_o) was 11.8 %. The proportion of polymorphic loci was 40 %. These values are clearly higher than those reported for most species of rodents in the northern hemisphere (Nevo et al. 1984). Ward et al. (1992) reported an average H value of 6.7 % for 172 species of mammals. Patton et al. (1989) found values ranging from 1.1 to 7.1 % for H and between 7.7 to 21.3 % for P in different species of the tribe Akodontini (subfamily Sigmodontinae, family Muridae) from Peru. The relatively high level of polymorphism observed in *C. hummelincki* is comparable to that of other sigmodontine species of the genera *Calomys* (Gardenal et al. 1980; Gardenal and Blanco, 1985; Gardenal et al. 1990; Garcia et al. 1990) and *Akodon* (Apfelbaum and Blanco 1985), and the species *Graomys griseoflavus* (Theiler and Gardenal 1994) and *Eligmodontia typus* (de Sousa et al. 1996) from Argentina (Tab. 2). Barrantes et al. (1993) found expected H between 3.8 and 11 % in populations of eight species of *Akodon* from Argentina. The last value corresponded to one population of *A. longipilis*. The observed H value was much lower (3.9 %), a result not explained by the authors.

Table 3 presents genetic distance values between *C. hummelincki*, *C. laucha*, *C. musculinus*, and *C. venustus*. On the basis of modified Rogers' distances (Wright 1978)

Table 1. Allele frequencies in the population sample of *Calomys hummelincki*

Locus	Allele	Frequency	Locus	Allele	Frequency
Es-1	94	0.91	Adh	91	1.00
	91	0.09	Mdh-1	100	1.00
Es-2	95	0.91	Aat-1	79	1.00
	87	0.09	Aat-2	27	1.00
Es-4	70	1.00	Idh-1	69	1.00
Es-5	82	0.43	Idh-2	100	1.00
	72	0.57	Ldh-1	96	1.00
Es-6	75	0.21	Gpdh	81	0.06
	50	0.79		71	0.47
Ndh	100	0.03	Mdh-2	100	1.00
	92	0.85	Acp_k	81	0.82
	85	0.12		70	0.18
Me	67	0.06	Acp_l	100	0.94
	48	0.94		94	0.06
Ldh-2	100	1.00	6Pgdh	a*	0.76
Sod	100	1.00		b	0.24
Cat	a*	0.71	Tf	a*	0.03
	b	0.23		b	0.44
	c	0.06		c	0.53

* Alleles at the loci not analyzed in other species of *Calomys* are designated by letters. The loci Ak, G6pdh, Pgm-1, Pgm-2, Sod-2, Hpt and Alb were monomorphic and not analyzed in other species of *Calomys*. Alleles at the remaining loci are designated by numbers, indicating electrophoretic mobilities of bands relative to those observed in other *Calomys* species by GARDENAL et al. (1990).

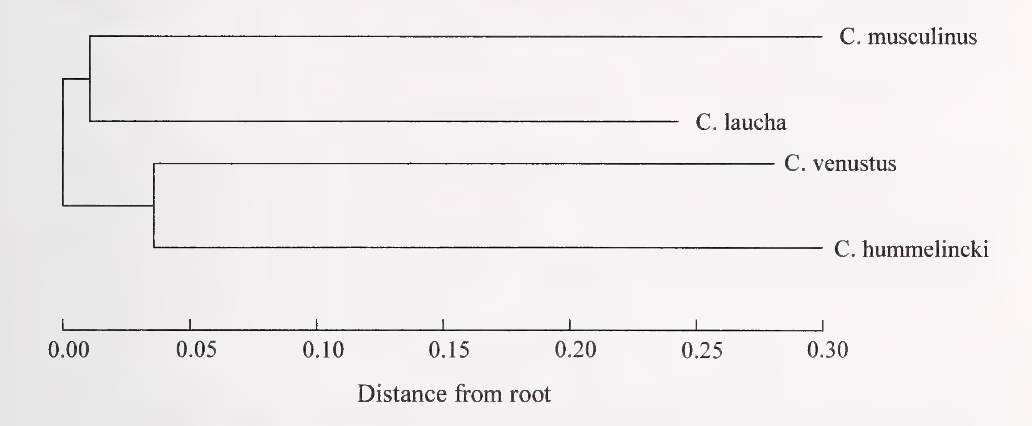
Table 2. Proportion of polymorphic loci (P) and expected heterozygosity (H_e) in different species of South American sigmodontine rodents.

Species	$P_{99\%}$	H_e	D_N^*	Reference
C. hummelincki	40	12.7	–	this study
C. laucha	62.5–77.3	11.8–16.3	0.002–0.010	GARDENAL et al. (1990) GARCIA et al. (1990)
C. musculinus	61.0–73.0	14.9–20.0	–	GARDENAL et al. (1980) GARDENAL and BLANCO (1985) GARDENAL et al. (1990)
C. venustus	66.7	14.6	–	GARDENAL et al. (1990)
Akodon dolores	27.8–38.9	13.8–19.2	–	APFELBAUM and BLANCO (1985)
Akodon azarae	16.6–30.0	9.9–11.8	–	APFELBAUM and BLANCO (1985)
Akodon (Peru)	7.7–21.3	1.1–7.1	–	PATTON et al. (1989)
Akodon (Argentina)	6.7–26.7	6.7–11	–	BARRANTES et al. (1993)
Eligmodontia typus	68.0	16.0	0.005–0.015	DE SOUSA and GARDENAL (1996)
Graomys griseoflavus	46.0–66.0	16.0–18.0	0.075–0.093	THEILER and GARDENAL (1994)
Oligoryzomys flavescens	34.6–61.5	5.8–9.7	0.0016–0.0088	CHIAPPERO et al. (1997)

* NEI's (1972) genetic distance between populations

Table 3. Values for modified Rogers' distance (D_R; above the diagonal) and Nei's genetic distance (D_N; below the diagonal) between species of *Calomys.*

	C. hummelincki	*C. laucha*	*C. venustus*	*C. musculinus*
C. hummelincki	**	0.470	0.530	0.591
C. laucha	0.289	**	0.516	0.510
C. venustus	0.378	0.360	**	0.578
C. musculinus	0.494	0.349	0.469	**



Cophenetic correlation = 0.994

Fig. 1. Distance Wagner procedure tree based on modified Rogers' distances between the species *Calomys hummelincki, C. laucha, C. venustus,* and *C. musculinus.*

the distance Wagner tree of figure 1 was constructed. *C. hummelincki* appears more closely related to *C. venustus* than to *C. laucha*. Table 2 includes values of D_N between populations of *C. laucha, E. typus*, and *G. griseoflavus*. These species belong to the same tribe (Phyllotini) as *C. hummelincki*. The highest D_N between populations of the same species was 0.09, while all comparisons between species gave values above 0.29.

The taxonomic status of the Venezuelan pigmy mouse (*C. hummelincki*) has been the subject of controversy (Perez Zapata et al. 1987). Hershkovitz (1962) did not recognize *C. hummelincki* as a separate species and considered it as *C. laucha*.

It was known that *C. laucha* was distributed in a wide area of South America comprising southeastern Brazil, southern Bolivia, Paraguay, Uruguay, and central Argentina. This is very far from the south of the region where *C. hummelincki* is found. When Hershkovitz (1962) proposed this species as a synonym of *C. laucha*, he assumed that its presence in Venezuela could be due to accidental transportation by man.

Data presented here strongly support the proposal that *C. laucha* and *C. hummelincki* are distinct species, providing thus a more rational explanation for the geographic distribution of the species. The genetic distance between *C. laucha* and *C. hummelincki* (D_N = 0.36) is within the range accepted for species which have completed their reproductive isolation (Ayala 1982). Five loci (Es-1, Es-4, Adh, Aat-1 and Gpdh) can be utilized as "diagnostic", since the species do not share alleles at these loci. Genetic distances for intraspecific comparisons between populations of *C. laucha, Eligmodontia typus*, and *Graomys griseoflavus*, species closely related to *C. hummelincki*, gave values below 0.09 (Tab. 2).

In an analysis of karyological relationships among species of *Calomys*, Vitullo et al. (1990) described different "groups" of species on the basis of chromosomal characteristics (2n, fundamental number, morphology). According to these criteria, *C. hummelincki* (2n = 60; FN = 64) and *C. laucha* (2n = 64; FN = 68) were included in the same group (Group I), while *C. venustus* (2n = 56; NF = 66) and *C. musculinus* (2n = 38; FN = 56) were included in different groups (II and III, respectively). The study of differentiation in structural genes presented here indicates different relationships between species of *Calomys* than those inferred from cytogenetic analysis. Nevertheless, it has been suggested that in mammals the rate of evolution of morphology, karyotype, and structural genes can be independent, and so the relationships assigned on the basis of these criteria may disagree (Schnell and Selander 1981; Apfelbaum and Reig 1989).

Aknowledgements

The authors thank Dr. Antonio Blanco for advice and critical revision of the manuscript. This work was supported, in part by grants from the Concejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina, the Consejo de Investigaciones Científicas y Tecnológicas de la Provincia de Córdoba (CONICOR) and the Antorchas Foundation. C.N.G. and B.A.G. are Career Investigators of CONICET and M.B.C. is a Fellow of CONICOR.

Zusammenfassung

Allozymvariation und taxonomische Stellung von Calomys hummelincki (Rodentia, Sigmodontidae)

Die genetische Variabilität einer Population von *Calomys hummelincki* aus Venezuela wurde mittels Gelelektrophorese von Enzymen und Serumproteinen untersucht. Insgesamt wurden 30 Genloci erfaßt. Die Polymorphierate betrug 40 % und der durchschnittliche erwartete Heterozygotiegrad (H_e) 12,7 %. Diese Werte liegen höher als jene der meisten bisher untersuchten Nagetierarten der Nordhemisphäre. Sie sind jedoch den Angaben über andere Arten der Unterfamilie Sigmodontinae aus Argentinien vergleichbar. Die genetischen Distanzen nach Nei (D_N) zu den Arten *C. laucha, C. venustus* und *C. musculinus* reichten von 0,289 bis 0,494, während jene zwischen Populationen der jeweiligen Arten einen Wert von 0,09 nicht überschritten. Ein auf modifizierten Rogers-Distanzen beruhender Wagner-Baum zeigt, daß *C. hummelincki* mit *C. venustus* näher verwandt ist als mit *C. laucha*. Unsere Daten stützen die Hypothese, daß *C. hummelincki* und *C. laucha* zwei verschiedene Arten sind.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

The karyotypes of *Cryptomys anselli* sp. nova and *Cryptomys kafuensis* sp. nova: new species of the common mole-rat from Zambia (Rodentia, Bathyergidae)

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Receipt of Ms. 04. 05. 1998
Acceptance of Ms. 19. 10. 1998

Abstract

Two new species of a "small form" (i. e. with body mass of about 90 g) of the African mole-rat *Cryptomys* (Rodentia: Bathyergidae) are described from Zambia: *C. anselli* sp. nova characterized by diploid chromosome number 2n = 68 from Lusaka Province and *C. kafuensis* sp. nova with 2n = 58 chromosomes from Itezhi-Tezhi, Kafue National Park, Southern Province. Conventionally stained, C- and G-banded karyotypes, and localisation of NORs are described for both species. Whereas classical morphological and morphometrical traits cannot be used for diagnosis of *Cryptomys* species, karyotypes and allozymes enable distinction of both new species from each other and from other known *Cryptomys* species. Nevertheless, also the thickness of the external wall of the infraorbital foramen (relative to the breadth of the opening) seems to be species-specific: it is thicker in the examined specimens of *C. anselli* sp. nova but thinner in *C. kafuensis* sp. nova.

Key words: *Cryptomys*, Bathyergidae, chromosome, subterranean mammals, taxonomy

Introduction

African mole-rats of the genus *Cryptomys* Gray, 1864 (Bathyergidae) are subterranean rodents occurring from semi-arid to mesic habitats in different soil types over a wide geographic range from Ghana to the Cape Province in South Africa. Although it is not a problem to recognize *Cryptomys* as *Cryptomys*, extreme variation in many morphological traits (cranial parameters, body size, pelage coloration) traditionally employed in alpha-taxonomy of rodents, makes taxonomic treatment of this genus very difficult. Accordingly, different authors recognize different numbers of species. Thus, for instance, 44 to 49 species of *Cryptomys* have been named by Allen (1939) or Ellermann (1940), respectively, whereas only three have been considered by Nowak (1991). More recently, Honeycutt et al. (1991) recognized seven species: *Cryptomys bocagei* (De Winton, 1897); *Cryptomys damarensis* (Ogilby, 1838); *Cryptomys foxi* (Thomas, 1911); *Cryptomys hottentotus* with subspecies *C. h. hottentotus* (Lesson, 1826), *C. h. natalensis* (Roberts, 1913), *C. h. darlingi* (Thomas, 1895); *C. h. amatus* (Wroughton, 1907), and *C. h. whytei* (Thomas, 1897); *Cryptomys mechowi* (Peters, 1881); *Cryptomys ochraceocinereus* (Heuglin, 1864); *Cryptomys zechi* (Matschie, 1900).

It has been repeatedly demonstrated (Rosevear 1969; Ansell 1978; Williams et al. 1983; Nevo et al. 1986, 1987; Honeycutt et al. 1987, 1991; Janecek et al. 1992) that classi-

0044-3468/99/64/01 – 036 $ 12.00/0

cal morphological qualitative and quantitative traits are not sufficient for the diagnosis of *Cryptomys* species, and additionally, cytology, serology, and molecular genetics should be taken into account. Subsequent karyological studies demonstrated that at least *Cryptomys darlingi* and *Cryptomy amatus* should be considered distinct species (Aguilar 1993; Macholán et al. 1998). In addition, our allozyme and karyotype studies (Filippucci et al. 1994, 1997; Macholán et al. 1993) identified two additional species of the small form of *Cryptomys* in Zambia characterized by karyotypes 2n = 58 (the "Itezhi-Tezhi population") and 2n = 68 (the "Lusaka population").

Particularly the Lusaka population (2n = 68) has been subjected to intensive research on various aspects of its biology: reproduction and social behaviour (Burda 1989, 1990, 1995; Begall 1997; Begall and Burda 1998; Willingstorfer et al. 1998), hearing, ear morphology, and vocalization (Müller and Burda 1989; Burda et al. 1992; Müller et al. 1992; Lindenlaub and Burda 1993, 1994; Lindenlaub et al. 1995; Kössl et al. 1996; Brückmann and Burda 1997; Credner et al. 1997), magnetic compass orientation (Burda et al. 1990; Marhold et al. 1997), aspects of neuroanatomy (Oelschläger and Burda 1992; Misek et al. 1996), physiology of metabolism (Marhold and Nagel 1995). Parasites in both species (and *C. mechowi*) have been studied by Scharff et al. (1996, 1997). In the meantime, the Zambian *Cryptomys* has become a well established model in many further biological studies. This fact calls for an unambiguous denomination of this species. While it has been obvious to us (and we have repeatedly stated it in all our publications) that these *Cryptomys* represent species distinctly different from South African *Cryptomys hottentotus* (for which they had been previously taken), a formal description has not been possible until the taxonomic status of neighbouring populations of *Cryptomys amatus* and *C. darlingi* had been clarified (Macholán et al. 1998; Aguilar 1993). While the species status and their distinction from other *Cryptomys* species have been proven in allozyme studies (Filippucci et al. 1994, 1997), in this study we denominate both species and describe their karyotypes in detail.

Material and methods

Altogether nine individuals of the Lusaka population (see below and Tab. 1) and three individuals (one male, two females) of the Itezhi-Tezhi population were karyotyped. Mitotic metaphases were obtained directly from bone marrow. Slides were differentially stained using the trypsin digestion (G-banding) technique by Seabright (1971) and the C-banding technique by Sumner (1972). Nucleolus organizer regions (NORs) were visualized by the silver-staining method of Howell and Black (1980).

Results

Cryptomys anselli **sp. nova**

Holotype
Adult male, whole body ethanol-preserved, in Senckenberg Museum, Frankfurt am Main, Germany, allocation number SMF 87018 (specimen's field number L-45). Collected on 15. 07. 1996 by Andreas Scharff.

Paratype
Adult female, SMF 87019 (L-46); sample data as in holotype.

Type locality
Court of the Chainama Hills Golf Club in the north-eastern part of Lusaka, Zambia.

Etymology
The species name recalls late Mr. W. F. H. Ansell and his merit in the study of taxonomy and distribution of mammals of Zambia.

Measurements and diagnosis
Body size and cranial measurements in *Cryptomys* have no taxonomic-diagnostic value and are not provided here (for reasoning see Discussion). The body mass of adult wild-caught individuals (which is the best parameter for comparing body size among different *Cryptomys* species) in *C. anselli* sp. nova amounts to 76 ± 12 g (range 65–102 g, n = 66) in females and to 96 ± 13 g (range 80–126 g, n = 20) in males. Pelage coloration is age- and body mass-dependent: it is dark slate grey and metallic black in sucklings, greyish brown in weaned pups, brown in juvenile and subadult animals, and eventually golden ochre in adults. There is a remarkable variation in the size and shape of the white head spot, nevertheless, it is well developed in most individuals. The infraorbital foramen is thick-walled (i. e. the external wall is thicker than the breadth of the opening), elliptical or drop-shaped (reference is made to specimens L6, L13, L15, L25, L48, L50, L54, Kenson 4, Kenson 9, Kenson 10, Kenson x, LX-3, LX6, and LX-13 deposited at the Department of General Zoology, University of Essen). However, it should be noted that lateral asymmetry in the shape of the infraorbital foramen was found in some specimens (L19, L23).

The analysis of allozymic variation allows clear separation of *Cryptomys anselli* sp. nova from *C. kafuensis* sp. nova, *C. mechowi*, *C. damarensis*, *C. h. hottentotus*, and *C. h. natalensis* and warrants attributing of a species status (Filippucci et al. 1994, 1997).

The diploid chromosome number in all the individuals examined (n = 9) is 2n = 68. The proportion of acrocentric and biarmed chromosomes is variable. The karyotype consists of mainly (56–59) acrocentric chromosomes, 2–4 large subtelocentric autosomes, 0–3 submeta- or metacentric autosomes, and 4–6 small biarmed autosomes (cf. Fig. 1, Tab. 1). The X chromosome is variable in size and centromeric position, and the two X chromosomes in female sets are often heteromorphic. The Y chromosome is dot-like, probably uniarmed. Consequently, NF is variable and ranges from 79 to 82. C-positive heterochromatic arms are observed in a varied number of large biarmed autosomes and in a small pair of subtelocentric autosomes. Centromeric dark bands are present in most chromosomes. Distinct telomeric dark C-bands are situated in one large submetacentric chromosome (presumably the X) and in six autosomal pairs. The Y chromosome stains positively in C-banded slides (Fig. 2). G-banding cannot reveal any clear homology among the large biarmed autosomes and the X chromosomes (Fig. 3). Ag-NORs are situated in the telomeric areas of one large biarmed chromosome, two small metacentric, and in about 10 acrocentric autosomes.

Table 1. Composition of individual karyotypes in the examined specimens of *Cryptomys anselli* sp. nova.

No.	protocol	sex	NF	NFa	large ST	large M/SM	small M/SM	a
1	MM240	M	79	75	3	0	6	57
2	MM241	F	79	75	3	0	6	57
3	MM242	F	80	76	4	1	5	56
4	MM243	M	79	75	2	1	6	57
5	JZ1051	F	80	76	2	2	6	56
6	MM329	F	81	77	4	1	6	55
7	MM870	F	81	77	4	2	5	55
8	MM871	M	82	78	3	3	6	54
9	MM872	F	80	76	4	2	4	56



Fig. 1 a.

Chromosomal slides are deposited in the Institute of Vertebrate Biology, Academy of Sciences CR, Brno, Czech Republic.

Distribution and habitat

The animals of this species were collected in cultivated fields, gardens, golf courses, and savannah-bushland habitats in Lusaka, Zambia, and its north-eastern suburbs (within and near the University of Lusaka campus), in Ngwerere (10 km north of Lusaka), Mungule (about 30 km north-west of Lusaka) and Chinunyu (about 90 km east of Lusaka), i.e., within the degree squares 1528 A1, 1528 A4, and 1529 A1 (following the mapping of ANSELL 1978). The collecting sites are characterized by the mean annual rainfall of 822 mm (monthly precipitation amounts to 68 ± 81 mm, range 0–207 mm).

***Cryptomys kafuensis* sp. nova**

Holotype

Adult female, whole body ethanol-preserved, in Senckenberg Museum, Frankfurt am Main, Germany, allocation number SMF 87124. Collected on 27. 05. 1991 by JIŘÍ KOČKA.

Paratype

Adult females, SMF 87125 and SMF 87126; sample data as in holotype.



Fig. 1b.

Fig. 1. Conventionally stained karyotypes of *Cryptomys anselli* sp. nova. a = individual No. 5 in table 2, b = individual No. 6.

Type locality
"Hot Springs" in Itezhi-Tezhi, Kafue National Park, Southern Province, Zambia, within the degree square 1526 C1 (following the mapping of Ansell 1978).

Etymology
The name of the species refers to the locality, the Kafue National Park in Zambia.

Measurements and diagnosis
The body mass of adult wild-caught individuals in *C. kafuensis* sp. nova amounts to 73 ± 9 g (range 61–77, n = 10) in females and to 113 ± 28 g (range 84–139, n = 3) in males. Pelage coloration and its age-dependent changes correspond to the situation described above for *C. anselli* sp. nova. The white head spot is well developed in most individuals and tends to be more prominent than in *C. anselli* sp. nova; nevertheless, its size and shape are individually very variable. The infraorbital foramen is thin-walled (i. e. its external wall is thinner than the breadth of the foramen), drop-like to elliptical (reference is made to specimens K6, K8, K10, K14 deposited at the Department of General Zoology, University of Essen).

The analysis of allozymic variation allows clear separation of *C. kafuensis* sp. nova from *Cryptomys anselli* sp. nova, *C. mechowi*, *C. damarensis*, *C. h. hottentotus*, and *C. h. natalensis* and warrants allocation of a species status (Filippucci et al. 1994, 1997).



Fig. 2 a.

The diploid chromosome number in all the individuals (n = 3) examined is 2n = 58, NF = 82. The karyotype consists of 11 biarmed and 17 acrocentric autosomal pairs. Four biarmed (one metacentric, two submetacentric, and one subtelocentric) autosomal pairs can be distinguished according to their larger size. The other biarmed (six meta- or submetacentric and one subtelocentric) pairs of autosomes are distinctly smaller. The two largest acrocentric pairs are approximately as large as the largest biarmed autosomes. One of these large acrocentric pairs possesses very short second arms. The other acrocentric autosomes are distinctly smaller and they form a continuum of decreasing sizes. The X chromosome is metacentric and its size is similar to the largest autosomes. The Y chromosome is dot-like, probably uniarmed (Fig. 4 a). The C-banded karyotype reveals considerable amounts of positively stained heterochromatin. One arm and the broad pericentromeric area of the largest metacentric autosome are completely heterochromatic. A heterochromatic small arm is visible also in the small subtelocentric pair. Centromeric dark bands are found in certain biarmed and in most of the acrocentric chromosomes. A telomeric C-positive band in one arm is situated in three pairs of biarmed and five pairs of acrocentric autosomes. Intercalary dark bands are situated in two acrocentric autosomes. The X chromosome is not positively stained in C-banded preparations, whereas the Y chromosome has a prominent dark band in the pericentromeric area (Fig. 4 b). The large metacentric autosome with the C-heterochromatic arm stains mainly negatively in G-banded preparations, and it possesses only one large dark band situated in the euchromatic arm. The G-banding pattern enables identification of most of the homologous chro-



Fig. 2 b.

Fig. 2. C-banded karyotype of *Cryptomys anselli* sp. nova. a = individual No. 5, b = individual No. 3.

mosomes (Fig. 4 c). The Ag-NORs positive signals are observed in the telomeric areas of several (10–12) small metacentric and acrocentric autosomes.

Chromosomal slides are deposited in the Institute of Vertebrate Biology, Academy of Sciences CR, Brno, Czech Republic.

Distribution and habitat

The animals of this species were collected in grassland habitats at the locality Hot Springs and cultivated fields of nearby villages, in Itezhi-Tezhi, Kafue National Park, Zambia, within the degree square 1526 C1 (following the mapping of ANSELL 1978). The collecting site is characterized by the mean annual rainfall of 787 mm (monthly precipitation amounts to 66 ± 78 mm, range 0–199 mm).

Discussion

Morphology and morphometry

As stated earlier *Cryptomys* mole-rats are remarkably polymorphic, so that it is not possible to provide unambiguous diagnostic morphological traits or measurements. As in other rodents, *Cryptomys* is characterized by indeterminate growth. However, the growth is not continuous and its rate is subjected to accelerations and periods of stasis depending on di-

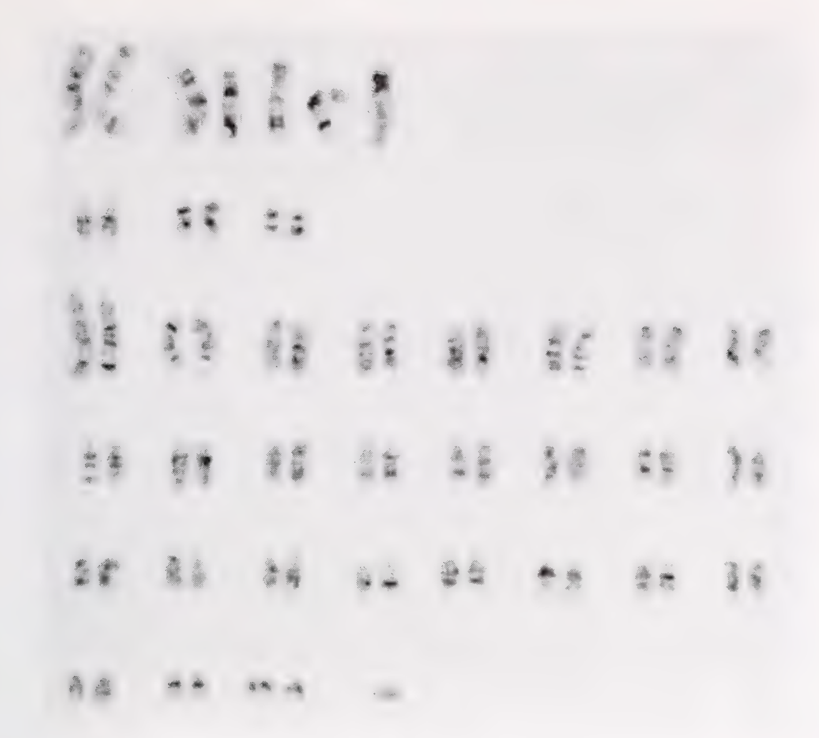


Fig. 3. G-banded karyotype of *Cryptomys anselli* sp. nova individual No. 5.

verse factors (reproductive and social status, age, and unknown factors). Due to these facts, the generally slow growth rate, and remarkable longevity (15 years and more), the body size and form and consequently also cranial proportions are subject to progressive and regressive changes (i. e. they fluctuate) during individual life (cf. BEGALL and BURDA 1998). For counting the mean adult body mass we selected individuals from our sample which weighed at least 60 g in females and 80 g in males. This arbitray limit is based on our long-term observation (BURDA 1989; 1990; BEGALL and BURDA 1998) of the lowest body mass of breeding animals in captivity. Whereas there is significant sexual dimorphism in body mass in both species, there is no significant difference in body mass of males or females between both species.

Whereas in all the examined skulls (n = 14, juveniles and adults, females and males being represented in the sample) of *C. anselli* sp. nova, the external wall of the foramen infraorbitale was relatively thick, all the examined skulls (n = 4, 2 adult males, 2 adult females) of *C. kafuensis* sp. nova were characterized by a thin-walled foramen. HONEYCUTT et al. (1991) considered thick-walled outer foramina to be characteristic of the *C. damarensis*, *C. mechowi*, and *C. bocagei* group (and west and central African species), while thin-walled foramina should characterize the *C. hottentotus* group. Consequently, *C. anselli* sp. nova should be grouped with *C. damarensis* and *C. mechowi*, whereas *C. kafuensis* sp. nova should be closer related with *C. hottentotus*. However, the results of allozymic studies (FILIPPUCCI et al. 1994, 1997) do not support such distinction. Moreover, it should be noted that our specimens of *C. mechowi* from Ndola exhibit the thin-walled condition.

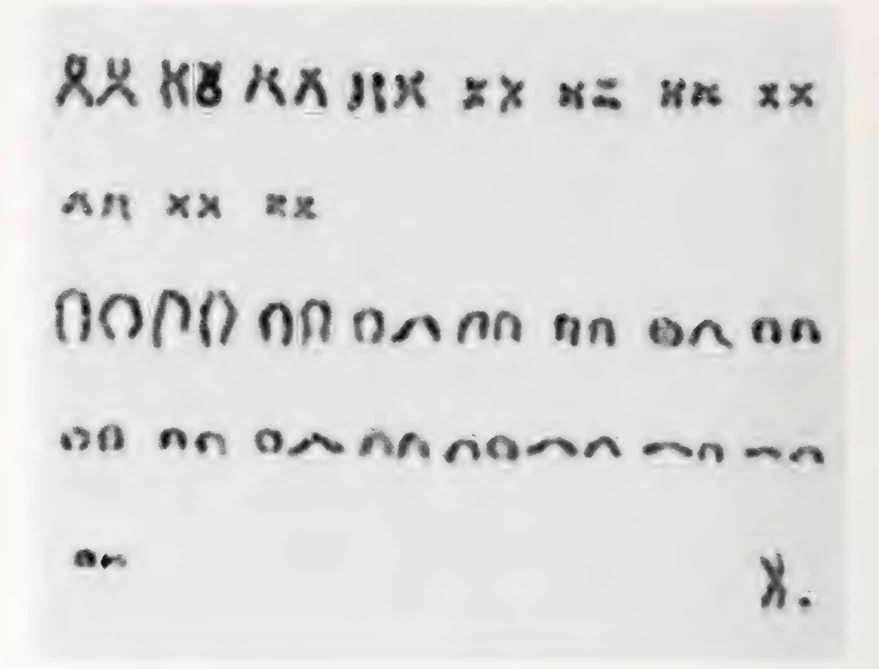


Fig. 4 a.



Fig. 4 b.

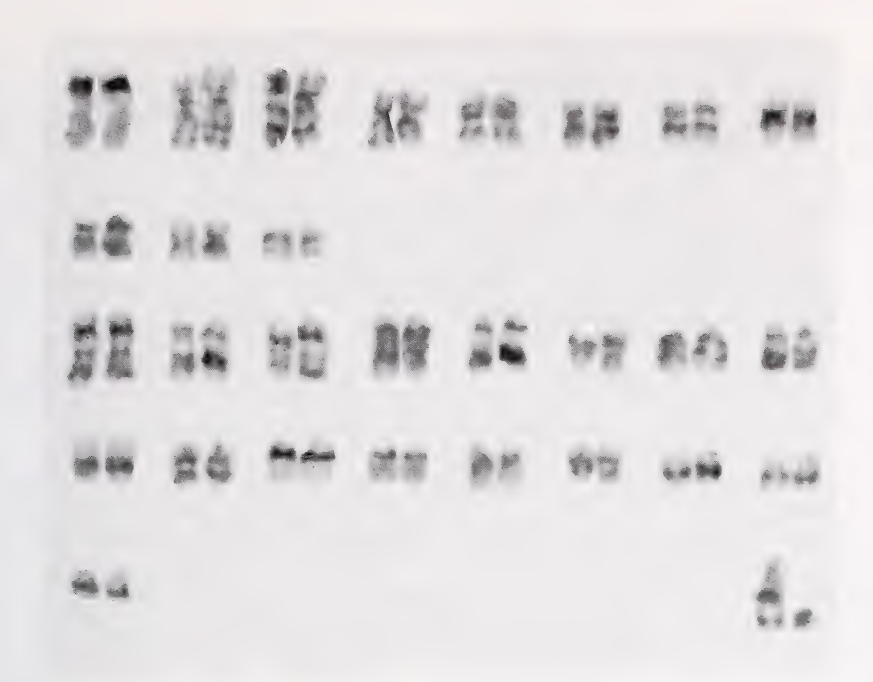


Fig. 4 c.

Fig. 4. Karyotypes of a male of *Cryptomys kafuensis* sp. nova. a = conventional staining, b = C-banding, c = G-banding.

Table 2. Characteristics of known karyotypes (representing different species) of *Cryptomys.* M – metacentric, SM – submetacentric, ST – subtelocentric, A – acrocentric, NF – fundamental number of chromosome arms in a female karyotype.

Species	Occurrence	Karyotype (2 n)	Autosomes			Sex chromosomes		Arms (NF)	Reference
			M, SM	ST	A	X	Y		
C. mechowi	Zambia (Copperbelt Province)	40	38			M/SM	SM	80	Macholán et al. (1993)
C. amatus	Zambia (Central Province)	50	42	2	4	M	A	96	Macholán et al. (1998)
C. h. hottentotus	South Africa (Transvaal)	54	50		2	SM	?	106	Nevo et al. (1986)
C. h. natalensis	South Africa (Natal)	54	48		4	SM	A	104	Nevo et al. (1986)
C. darlingi	Zimbabwe (Harare)	54	28		24	A	M	82	Aguilar (1993)
C. kafuensis	Zambia (Southern Province)	58	18	4	34	M	dot	82	present study
C. foxi	Cameroon	66 (70)	58		6	SM	M	130 (138)	Williams et al. (1983)
C. anselli	Zambia (Lusaka Province)	68	6–9	2–4	56–59	M	dot	79–82	present study
C. damarensis	Botswana (Kalahari)	78	16		60	M	SM	96	Nevo et al. (1986)

Karyotype

In addition to the results of allozymic studies (Filippucci et al. 1994, 1997), also distinct numbers and morphology of the chromosomes substantiate distinguishing of *Cryptomys anselli* sp. nova and *C. kafuensis* sp. nova from other species of the genus and from each other.

The variation in the number of biarmed autosomes in *Cryptomys anselli* sp. nova is presumably due to changes in the number of heterochromatic arms. Regarding the difficulty in establishing homologies between the affected pairs according to the G-banding pattern, it is probable that also other unknown mechanisms were involved. Differences in the number of biarmed autosomes probably result from additions and/or deletions of the C-heterochromatic arms. The variation is interindividual and no consistent differences were found between the specimens collected in different localities. The G-banding pattern in the metacentric autosome with the whole-heterochromatic arm in *Cryptomys anselli* sp. nova seems similar to the analogous chromosome in *C. kafuensis* sp. nova.

The similar fundamental numbers of chromosomal arms found in *Cryptomys anselli* sp. nova, *C. kafuensis* sp. nova, *C. darlingi*, and *C. mechowi* (cf. Tab. 2) suggest Robertsonian rearrangements as a possible mechanism of chromosome speciation and indicate that different chromosomal fusions might have taken place in the evolution of individual lineages. Quantitative heterochromatin changes certainly played an important role in karyotype differentiation in this group. This is demonstrated also by an unusual extent of interindividual heterochromatin variation within the *Cryptomys anselli* sp. nova populations. A large metacentric autosome with the whole-heterochromatic arm is apparently stable in the 2n = 58 karyotype; however, its presumable homologue in the 68-chromosome karyotype is polymorphic.

Unfortunately, the high chromosome number and low G-band resolution level achieved in the preparations studied do not allow direct comparison between both karyotypes, or between them and other karyotypes known to date in the genus *Cryptomys*.

Taxonomy of Zambian *Cryptomys*

Following species and subspecies of *Cryptomys* have been formally described and named by previous authors from (what is now) Zambia and across borders (cf. Allen 1939, and see Fig. 5):

1. *Cryptomys darlingi* (Thomas, 1895) from surroundings of Harare (Salisbury), Zimbabwe, reference grid 1731-C. *Cryptomys darlingi* was considered a subspecies of *C. hottentotus* by Honeycutt et al. (1991). Although having the same chromosome number (2n = 54), composition of its karyotype is distinctly different (cf. Tab. 2) and warrants a species status (Aguilar 1993). The karyotype is distinct from karyotypes of Zambian *Cryptomys* studied to date.

2. *Cryptomys micklemi* (Chubb, 1909) from the Kataba river region, reference grid 1523-A, was considered a subspecies of *C. damarensis* by all subsequent authors. The animals from the type locality should be examined to check their taxonomic status.

3. *Cryptomys molyneuxi* (Chubb, 1908) from Luano Valley. This is a valley through which the combined Lunsemfwa and Mulungushi rivers flow after breaking through the Muchinga Escarpment (reference grids 1429-C to 1430-C, the exact type locality remains unknown – cf. Ansell 1978). A. Scharff (1996 unpubl. results) has found no evidence of *Cryptomys* in the reference grid 1429, where *Cryptomys* is obviously replaced by *Heliophobius* (cf. also Ansell 1978). This would imply that the type locality has to be searched for in the eastern part of the Valley, actually nearer to the type locality of *C. amatus* than to *C. anselli* sp. nova. It should be noted that all the subsequent authors have considered *C. molyneuxi* a synonym of *C. amatus*.

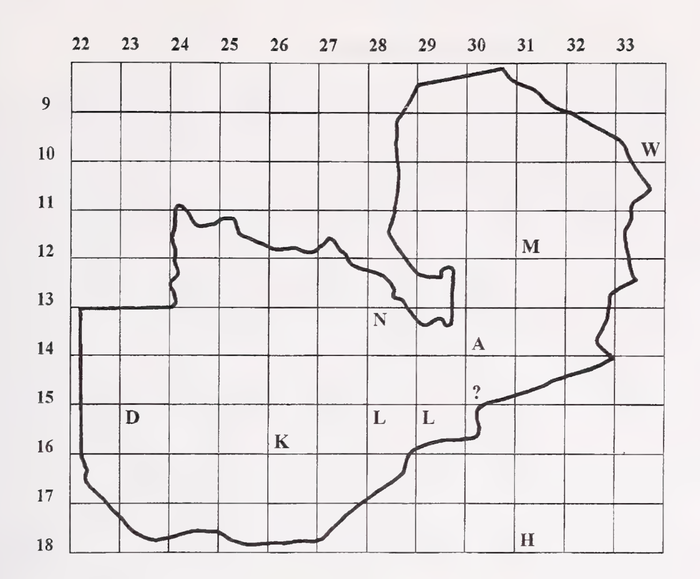


Fig. 5. Type localities of *Cryptomys* taxa described from (what is now) Zambia and extralimitally. H = *C. darlingi*, D = *C. damarensis micklemi*, K = *C. kafuensis* sp. nova, L = *C. anselli* sp. nova, ? = *C. hottentotus molyneuxi* = *C. amatus*, A = *C. amatus*, N = *C. mechowi* (2 n = 40, from Ndola), M = *C. mechowi mellandi*, W = *C. whytei.*

4. *Cryptomys amatus* (Wroughton, 1907) from the Alala Plateau (reference grid 1330-C) was considered a subspecies of *C. hottentotus* by subsequent authors. Faulkes et al. (1997) and Bennett and co-authors in their studies on *Cryptomys* contributed to the puzzle in calling *Cryptomys* from Lusaka *C. h. amatus*, even when citing our studies, implying that this is a name used by us to denominate Lusaka populations. This is, however, not true as we have reported these mole-rats as *Cryptomys* sp. (2 n = 68, Lusaka population) and always mentioned the taxonomic and nomenclature problems. Recently, we have collected mole-rats from the type locality of *C. amatus* and showed that they are different from *Cryptomys* from Lusaka and from *C. hottentotus* and deserve a species status of their own (Macholán et al. 1998).

5. *Cryptomys mellandi* (Thomas, 1906) from Mpika (reference grid 1131-C) was considered a subspecies or synonym of the giant mole-rat, *C. mechowi.* We have collected *C. mechowi* in Ndola (refrence grid 1328-B). It has still to be checked whether the Ndola giant mole-rats and *C. (mechowi) mellandi* are taxonomically identical. Giant mole-rats are not only morphologically (body size) but also karyologically (Macholán et al. 1993), though less allozymatically (Fillippucci et al. 1997), distinct from the smaller forms of *Cryptomys.*

6. *Cryptomys whytei* (Thomas, 1897) from Karonga, Malawi (reference grid 0933-D) was considered a subspecies of *C. hottentotus* by subsequent authors. Although we have not examined mole-rats from the type locality, we have studied karyotypes of single individuals from Kasama (ref. grid 1031-A) (Burda and Kawalika unpubl.) and from Malawian Nyika (1033-B) (Burda and Chitaukali unpubl.). Animals from both localities are chromosomally clearly distinct from each other and from all other *Cryptomys* studied to date.

Based on these facts we can exclude the possibility that *Cryptomys anselli* sp. nova from Lusaka and *Cryptomys kafuensis* sp. nova from Itezhi-Tezhi would represent just synonyms of already described species or subspecies.

Speciation "hotspot" in Zambia?

The earlier studies of karyotypes in bathyergids indicated, in contrast to the situation in many other subterranean rodents (particularly spalacids and ctenomyids) remarkable chromosome stability and conservatism. Thus, only one karyotype (2n = 60, GEORGE 1979) was described in the eusocial naked mole-rat (*Heterocephalus glaber*), distribution of which covers 14 latitude degrees; two karyotypes (2n = 60, GEORGE 1979; 2n = 62, own unpubl. data) are known in solitary *Heliophobius argenteocinereus*, distributed across 18 latitude degrees, and three chromosome species of *Cryptomys* were defined in the Southern African subregion, covering about 17 latitude degrees: 2n = 78 (or 74) in *C. damarensis* and 2n = 54 in *C. hottentotus* (NEVO et al. 1986); and 2n = 54 in *C. darlingi* (AGUILAR et al. 1993).

Contrary to those earlier findings on bathyergids from other regions of Africa, only in Zambia, within a relatively narrow belt covering 3 degrees of latitude, we have identified already four distinct karyotypes, representing four different species of *Cryptomys*: 2n = 40 (MACHOLÁN et al. 1993), 2n = 50 (MACHOLÁN et al. 1998), 2n = 58, and 2n = 68 (present study). Since only few populations were studied within the given belt and since Zambia itself extends from north to south over ten latitudes, many more karyotypes are expected to occur there (and our pilot studies confirm this prediction). Systematic faunistic, taxonomic, and ecological study of *Cryptomys* in Zambia (and neighbouring Malawi) will be of high interest for assessment of chromosomal evolution in this "hotspot" region and its historical/ecological causes, compared to relative stability in the Southern Africa subregion.

Acknowledgement

We thank D. KOCK for his comments on the manuscript and his advice. Assistance in the field by J. KOČKA and late S. KRUNIČ is highly appreciated. This study was partly supported by a travel grant from the DAAD to A. S., the grant (no. VS97102) of the Ministry of Education of the Czech Republic to J. Z. and M. M., and the grant from the research pool of the University of Essen to H. B.

Zusammenfassung

Die Karyotypen von Cryptomys anselli sp. nova und Cryptomys kafuensis sp. nova: neue Arten des Graumull von Sambia (Rodentia, Bathyergidae)

Zwei neue Arten von Graumullen, *Cryptomys* (Rodentia: Bathyergidae), der „Kleinform" (um ca. 90 g) werden von Sambia beschrieben: *C. anselli* sp. nova, charakterisiert durch die diploide Chromosomenzahl 2n = 68 von der Lusaka-Provinz, und *C. kafuensis* sp. nova mit 2n = 58 Chromosomen von Itezhi-Tezhi, Kafue-Nationalpark, Süd-Provinz. Konventionell gefärbte Karyotypen, einschließlich der C- und G-Bänderungsmuster, als auch die Lokalisation der NORs werden für die beiden Arten beschrieben. Während die klassischen morphologischen und morphometrischen Merkmale eine Artdiagnose bei der Gattung *Cryptomys* nicht ermöglichen, unterscheiden die Karyotypen und Allozyme die beiden neuen Arten voneinander und von anderen bekannten Arten der Gattung *Cryptomys*. Die Dicke der Außenwand (verglichen mit der Breite der Öffnung) des Foramen infraorbitale scheint artspezifisch zu sein: die Wand ist dicker bei allen untersuchten Exemplaren von *C. anselli* sp. nova und dünner bei *C. kafuensis* sp. nova.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Spacing among Harbour seals (*Phoca vitulina vitulina*) on haul-out sites in the Wadden Sea of Niedersachsen

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Receipt of Ms. 25. 05. 1998
Acceptance of Ms. 16. 10. 1998

Key words: *Phoca vitulina*, spacing, haul-out, Wadden Sea

Harbour seals haul out on sandbanks, on rocks or on ice, where they form loosely gregarious herds with little visible social interaction (BIGG 1969; GODSELL 1988; DA SILVA and TERHUNE 1988). In contrast to other pinniped species, such as elephant seals or walrus, they avoid close body contact when hauled out and defend their individual space by aggressive behaviour (BIGG 1981). Their grouping together is believed to be an anti-predator adaptation, granting more safety as well as more rest for the individual (TERHUNE 1985).

In the Wadden Sea no natural predators are known and hunting was stopped in 1972. However, during the summer months most of the Wadden Sea is used intensively as a recreational area. This leads to high antrophogenic disturbance pressure at a vulnerable time when the seals breed and moult. The objective of the present study was to document the spacing of harbour seals in order to provide basic information for future conservation measures.

In 1989 and 1990 a total of 17 survey flights were performed in Niedersachsen. All seal groups on the sandbanks were photographed at altitudes of 150 m. A Canon AE1 and Nikon F801 with a zoom of 35–200 mm and 100–200 ASA films were used. The shortest distance of each seal to its nearest neighbour was determined in "seal length" (SL). The length of the 3 largest seals was averaged on each projected slide, one SL being approximately 1.5 m (TRAUT 1997). Within each group, the distance to the nearest neighbour was classified as < 1 SL, 1–2 SL, > 2–3 SL, > 3–5 SL and > 5–10 SL. The midpoints of the classes were used for further calculations. All seals lying up to 10 SL apart were defined as belonging to one group. To investigate group size related variations in spacing, groups of 2–10, 11–20, 21–30, 31–50 seals (n = 20 each) and of > 50 seals (n = 13) were analysed (Spearman rank correlation). Regional differences were investigated by comparing groups of 50–60 seals in the east, middle, and west (n = 4 groups for each region) of the study area. Because mother-pup pairs keep close body contact, they were regarded as one unit. Therefore, distances to the nearest neighbour were measured from the mother seal only. The orientation of seals in relation to the waterline was examined by allocating the direction of the seals body to one of four 90° segments. The segments were numbered clockwise, with segment I (315°–45°) being opposite the waterline, segment II (45°–135°) and segment IV (225°–315°) being sideways. A seal facing the water would be allocated to segment III (135°–225°).

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The spacing of hauled out harbour seals resulted in an average distance of 2.7 ± 0.5 SL (n = 2 584) in 1990 and 2.5 ± 0.2 SL (n = 2 094) in 1989. In general, we found that 27% of the seals kept a distance of less than 1 SL, 42% were 1–3 SL, and 31% were more than 3 SL apart. We found that mother-pup pairs remained within the seal groups, but they kept a distance of 3.8 ± 2.1 SL (n = 439) on average.

In our study area the seal groups were predominantly small with an average of 11 ± 16 seals (range 1–138 seals). The influence of group size on spacing was investigated by comparing the average distance in groups of various sizes. In groups of more than 50 seals the individuals were significantly ($r_s = -0.6$) closer to each other than in smaller groups (3.2 SL for < 10 seals, 2.4–2.5 SL for 11–20, 21–30, 31–50 seals and 1.9 SL for > 50 seals).

Regional differences were investigated by comparing groups of similar size (50–60 seals) on haul-out sites in the east, middle, and west of the study area. In the western part the individual distance was 1.1 ± 0.2 SL on average. About double the distance was found in the middle and the eastern part with 2.4 ± 0.3 SL and 2.9 ± 0.8 SL, respectively.

The seals occupied only a fraction of the emerged sandbanks. Generally they hauled out in a single line along the water edge. Often track marks in the sand indicated that the seals had moved from higher positions towards the waterline. We found that 54.6% of the seals (n = 3 364) were facing the water (section III).

Seals in our study area kept an average distance of 2.5 SL (approximately 3.7 m) to their nearest neighbours. This varied in different areas, with seals being closer together in the western part of Niedersachsen. Even though quantification of disturbance pressure was not subject of this study, there is evidence, that especially in this area disturbance pressure is quite high during summer (TRAUT 1997). In Schleswig-Holstein, BACH and CLAUSS (1989) reported a decrease in spacing with an increase of disturbance level.

Female seals with pups did not separate from the group but the distance to other seals was larger. This is not surprising since it is known that females with pups are more susceptible to disturbances and react more aggressively than other seals (DRESCHER 1979).

We found an inverse relationship of individual spacing to group size in that seals were more densely packed in large groups. Similar results were found in a study in Schleswig-Holstein, where individual spacing decreased with increasing seal numbers (BACH and CLAUSS 1989). Since we did not observe a limitation of haul-out space, the closer grouping together could be related to higher disturbance pressure. When animals are closer packed, alarm signals from other seals could be detected faster. In Canada, large groups always had at least one vigilant animal, whereas groups of eight or fewer seals were observed to have no scanning individuals on occasion (DA SILVA and TERHUNE 1988). Taking this information, we can presume that with an average of 11 seals in Niedersachsen, at least always one of the seals is scanning the area. In our study about half of the observed seals were facing the water, which is higher than one would expect if the seals were oriented randomly. This could be another indication for disturbance pressure because it allows the seals a fast escape into the water. However, in order to quantify this, comparison with undisturbed areas would be needed, which, at this stage, we do not have.

Disturbance is an important criteria of habitat quality. If the level of disturbance influences the haul-out behaviour of seals, individual spacing as well as orientation could be used (additionally to other criteria) in judging the quality of haul-out sites.

We are obliged to the Bezirksregierung Weser-Ems and Landesjägerschaft Niedersachsen for the permission to participate in their survey flights. We thank the people who helped photographing the seals. The project was financed by Niedersächsisches Ministerium für Wissenschaft und Kunst Kap. 0608, FT 74.

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Observations on the occurrence of Irrawaddy dolphin, *Orcaella brevirostris*, in the Mahakam River, East Kalimantan, Indonesia

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Receipt of Ms. 16. 06. 1998
Acceptance of Ms. 30. 10. 1998

Key words: *Orcaella brevirostris*, Irrawaddy dolphin, Mahakam River, encounter rates, distribution

The Irrawaddy dolphin, *Orcaella brevirostris* (Gray, 1866), is considered a 'facultative' river dolphin of which distinct riverine and coastal, marine populations exist. The species is mainly found in shallow coastal waters of the tropical Indo-Pacific, but also in major river systems, in particular: Irrawaddy, Mekong, Mahakam, and the estuaries of the Ganges and Brahmaputra (Thomas 1892; Lloze 1973; Leatherwood et al. 1984; Marsh et al. 1989).

Relatively few published studies exist pertaining specifically to the population of Irrawaddy dolphins, in the local vernacular referred to as Pesut, in the Mahakam River, East Kalimantan, Indonesia. Studies so far have focused on the distribution and daily movement pattern of the species in Semayang-Melintang Lakes and connecting Pela and Melintang tributaries (Priyono 1994) and on bioacoustics (Kamminga et al. 1983). Although no systematic surveys on their abundance have been conducted so far, the Indonesian Directorate General of Forest Protection and Nature Conservation reported the existence of a population of 100–150 individuals for Semayang Lake, Pela River, and adjacent Mahakam River (Tas'an and Leatherwood 1984) while an unpublished estimate of 68 individuals in the Mahakam River was reported by Priyono (1994).

In this study, I present results of a preliminary survey, which was conducted on the Mahakam River, its tributaries, and adjacent lakes in East Kalimantan, Indonesia. Two surveys were conducted, both at medium to low waterlevels, the first from 27 February till 9 March 1997 and the second from 21 March till 6 April 1997. The river was surveyed using a small motor boat, occasionally by large public boat and by large and small motorized canoes, from Muara Kaman (ca. 200 km upstream) to Burit Hacau, at the rapids past Long Bagun (ca. 600 km upstream). In addition, the Semayang, Melintang, and Jempang Lakes were surveyed as well as the Pela, Melintang, and Kedang Pahu tributaries. The total survey length was 1 085 km. For analysis of sighting frequencies, the river was divided into a lower (from Samarinda, ca. 100 km upstream, until Muara Kaman), middle (from Muara Kaman until Long Iram, ca. 490 km upstream), and upper section (from Long Iram until the rapids after Long Bagun). Tributaries and lakes surveyed were also analysed separately.

Encounter rates were calculated for each section by dividing the number of observed dolphins by the number of kilometers searched. For testing whether the sighting frequencies are homogeneously distributed over all sections, and whether significant differences exist between different sections, G-tests of goodness of fit for single classification fre-

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quency distributions were used. To obtain a better approximation to x^2, Williams' correction to G was applied (G_{adj}; SOKAL and ROHLF 1981). G values were compared with critical values of the chi-square distribution (table C in SIEGEL and CASTELLAN 1988). Because multiple tests were performed, a corrected alpha of 0.01 was used in place of the nominal alpha of 0.05 (RICE 1989). Dolphins were spotted by eye and by means of binoculars. Group composition, location, diving times, respiration rates, and behaviors were recorded and photos taken. Additional data on the occurrence and status of Pesut were collected by interviewing local inhabitants, mainly fishermen.

During the present study, a total of 32 dolphins were observed, of which four were juveniles. During the first survey 29 individuals were encountered while during the second only 3 were observed, presumably because more time was spent in the upper section of the Mahakam, where no dolphins were observed. Group size varied from 3 to 7 animals with a median group size of 4 individuals. No minimum estimate of abundance could be made as only three dolphins were identifiable individually on the basis of their dorsal fin (no systematic photos of their dorsal fin were made). Also, there is the possibility that the dolphins might have been encountered more than once during each survey, in case they were heading in the same direction during the night as we were heading during the day. Irrawaddy dolphins were found to be rather inconspicuous; they do not leap high out of the water and may stay submerged for up to 12 minutes, surfacing only briefly. Except for some noises produced with their blow holes, which could be heard over 100 m distance, no audible whistles or pure tones were heard. Pesuts appeared to be very social, continously staying in close contact with one another, regardless of whether they were milling (feeding), travelling, or resting.

Table 1 shows the encounter rates, i. e. the number of dolphins per km of river searched, for different sections of the Mahakam River sytem. The dolphins are not homogenously distributed over the whole length of different river sections, tributaries, and lakes ($G_{adj} = 47.8$, df = 4, $p < 0.01$). The encounter rates of the middle river section are significantly higher than those of the upper section ($G_{adj} = 39.2$, df = 1, $p < 0.01$). Significantly higher encounter rates were also found for the tributaries when compared to the combined main river sections ($G_{adj} = 8.3$, df = 1, $p < 0.01$). However, all tributary observations of Pesut were made in the relatively short Pela tributary (only 8 km search effort), a connecting tributary to Semayang Lake and the Mahakam River. No sightings were made in the longer tributary Kedang Pahu of which 65 km in total was searched. No significant differences were found between encounter rates of middle river section and tributaries. As all tributary observations were made in the Pela tributary connecting to the middle section of the main river, and observations in the middle section of the Mahakam were significantly higher than in the upper section (with a higher search effort), this section presumably forms the primary habitat for the dolphins, when waterlevels are medium to low.

Encounter rates for the Semayang and Melintang Lakes, though lower, were not significantly so, when compared to the combined rates of the river and tributaries

Table 1. Encounter rates – dolphins observed per km of river searched.

Section	Search effort (km)	N of individuals	Encounter rate N of indiv./km
Lower Section	20	0	0
Middle Section	432	25	0.06
Upper Section	505	0	0
Tributaries	78	7	0.09
Lakes	50	0	0

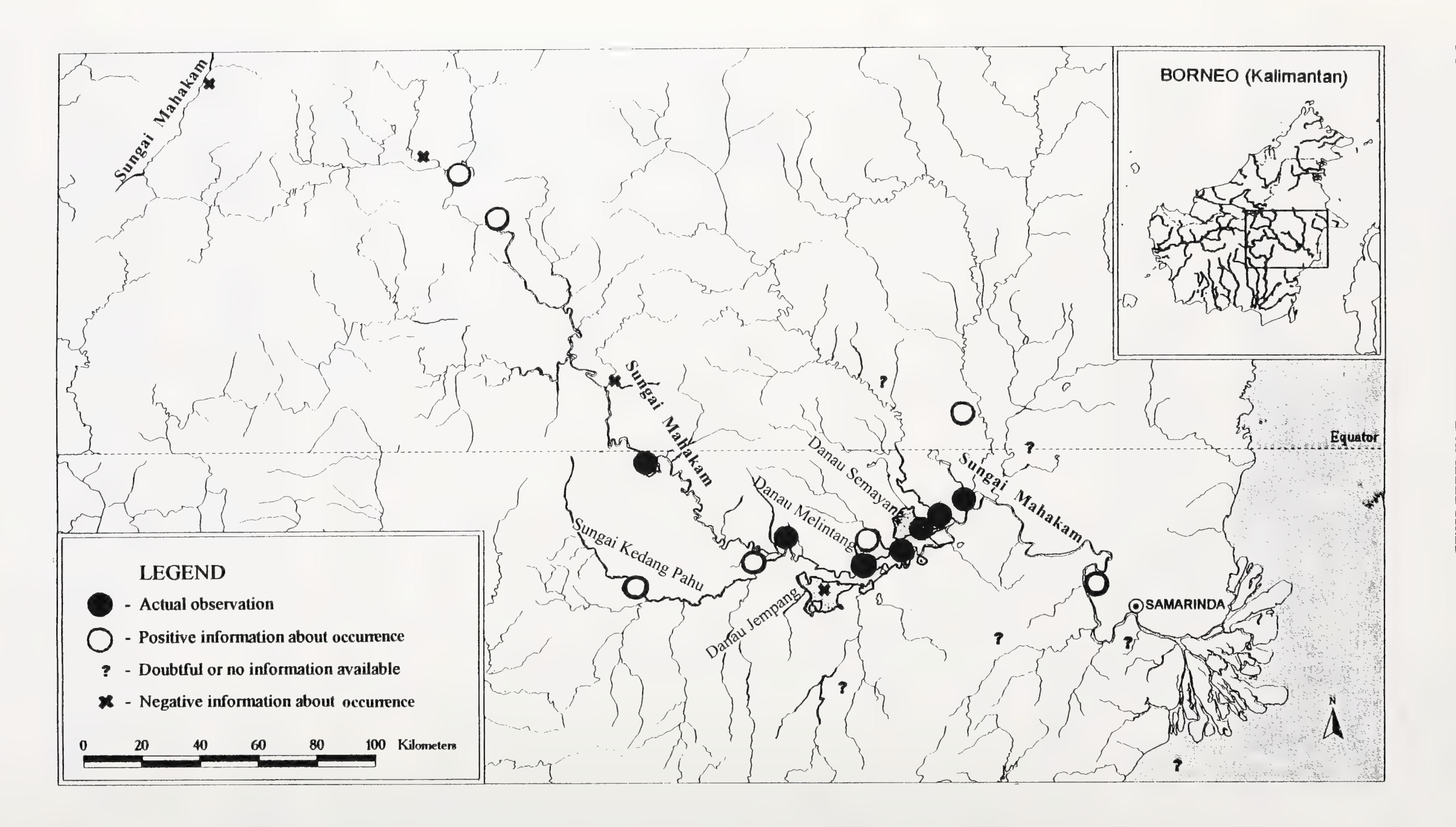


Fig. 1. Distribution of *Orcaella brevirostris* in the Mahakam River, East Kalimantan, Indonesia.

($G_{adj} = 3.9$, $G_{0.01} = 6.6$). The significant difference in encounter rates between these sections is probably a result of treating dolphins sightings in the Pela tributary as tributary observations. However, the dolphins' presence in either the Pela tributary or in Semayang Lake might depend on time of the day, as the dolphins are reported to migrate daily between these areas (PRIYONO 1994). The absence of observations of dolphins in the lakes most certainly is due to the fact that only 50 km were surveyed of the 10.300 hectares and 8.900 hectares large Semayang and Melintang Lakes, respectively. No significant differences in encounter rates were found between lower and other river sections, possibly due to the low search effort in this section.

The encounter rates found for *Orcaella brevirostris* in the Mahakam River are in the same order of magnitude as that reported for *Lipotes vexilifer* in the Yangtze River (0.09 dolphins/km), a population considered to have a high exctinction risk (HUA and CHEN 1992). However, the encounter rate of 0.06 dolphins/km in the mainstem Mahakam River, is considerably lower than those recorded, at similar medium-low water level conditions, for *Inia geoffrensis* and *Sotalia fluviatilis* in the mainstems of the Amazon-Marañon-Ucayali (0.18 and 0.27 dolphins/km, respectively; LEATHERWOOD 1996).

In the present study, Pesuts were observed up till Tering, 400 km upstream (Fig. 1), but they are said to occur up till the waterfalls after Long Bagun. Although no sightings were made in any of the lakes visited, Pesut has frequently been recorded in Semayang and Melintang Lakes (TAS'AN and LEATHERWOOD 1984), but the dolphins are said to be absent from Jempang Lake. Whether the Pesut occurs between Samarinda (near the mouth of the river) and the open sea, and in which of the river's tributaries, remains unclear. When water levels are high, dolphins are often observed by local inhabitants high up the Kedang Pahu tributary, past the village of Damai. Although the dolphins always moved away from our research vessel, they were observed twice near two villages (Muara Pahu and Tering) with high levels of boat traffic. According to local fishermen, they were said to frequent these places almost on a daily basis, presumably because of the higher availability of fish.

In conclusion, the results from this preliminary survey seem to indicate that encounter rates of the Irrawaddy dolphin in the Mahakam River are relatively low and fall in the same class of those recorded for the seriously threatened *Lipotes vexilifer*. Furthermore, middle sections of the river seems to be the primary habitat of Pesut, at least at medium to low water levels. Given the many factors contributing to possible deterioration of dolphin habitat (e. g. pollution from mining, forest fires, logging, and siltation), these observations of low encounter rates merit further study.

Acknowledgements

I wish to thank the East Kalimantan nature conservation authorities, sub Balai Konservasi Sumber Daya Alam, WWF-Indonesia, and WWF-Netherlands for their support and cooperation. My special thanks go to Ir. A. M. RACHMAT, D. SUPRIJONO, F. BUTCHER, and boatsman PAK SEGA, who all participated in the survey. I would like to thank Dr. P. J. H. VAN BREE for all his help and support throughout the study, as well as for his comments on the manuscript. Dr. C. J. HAZEVOET, Dr. A. Ø. Mooers, V. Nijman, and an anonymous reviewer are also thanked for their comments on this manuscript. I. LYSENKO and the World Centre for Monitoring Cambridge are thanked for drawing of the map.

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INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

First cytogenetic analysis of the genus *Bibimys* (Cricetidae, Rodentia)

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Receipt of Ms. 07. 01. 1998
Acceptance of Ms. 20. 04. 1998

Key words: *Bibimys*, Scapteromyini, cytogenetics

The South American Scapteromyini (Rodentia: Cricetidae), comprise three genera: *Scapteromys* with two species (*S. tumidus* and *S. aquaticus*), *Kunsia* with two species (*K. principalis* and *K. fronto*), and *Bibimys*, also with two species (*Bibimys torresi* and *Bibimys labiosus*) (WALKER 1964; BRUM-ZORRILLA et al. 1986).

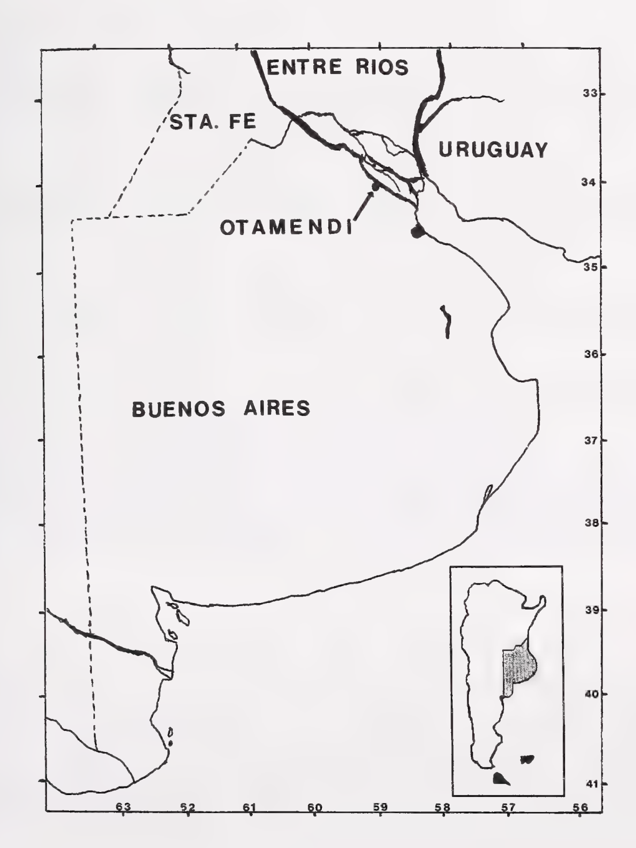


Fig. 1. Map of collection locality of *Bibimys torresi.*

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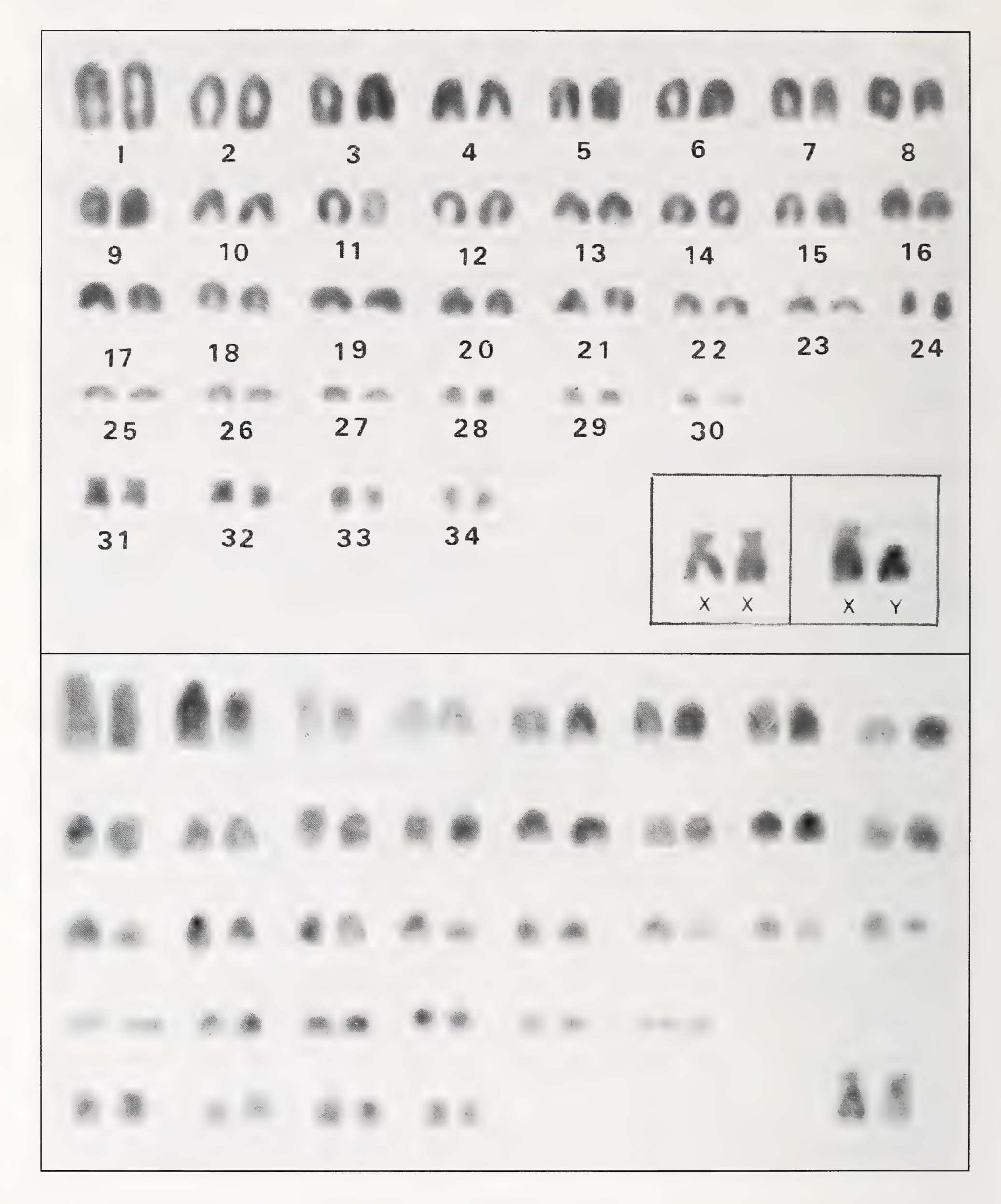


Fig. 2. Karyotype of *Bibimys torresi.* Giemsa stained (top), C-band pattern (bottom).

Scapteromys and *Bibimys* share the same semi-aquatic niche, whereas the giant rat *Kunsia* inhabits a semi-subterranean niche. It is mentioned that, since the Scapteronyini share a great affinity with the Akodontini in the pattern of the molars, the adaptation to different habitats of *Scapteromys*, *Bibimys*, and *Kunsia*, might have developed from an akodontine ancestral stock which invaded the lowlands of the Chaco region and later on expanded towards the east (Reig 1984). Nowadays there are no records of living specimens of *Bibimys labiosus* whereas *Bibimys torresi* has been collected in sites restricted to the delta of the Parana river in the Buenos Aires Province of Argentina. Neverthe-

less, the finding of fossils of *Bibimys* specimens at Lagoa Santa, Brazil (Voss and Myers 1991) and Cueva Tixi and Centinela del Mar, Argentina (Pardiñas 1995), shows that in the late Pleistocene and Holocene, the area of distribution of this genus was larger than today.

The taxonomic relationships among the genera of the Scapteromyini, were based on the evaluation of morphological similarities. Until recently, cytogenetic information was available only for *Scapteromys* species, while the karyotypes of *Kunsia* and *Bibimys* were still unknown. Here we present the standard and C-banded karyotype of *Bibimys torresi*, a species described for the first time by Massoia (1979).

Two females and one male of *Bibimys* were collected at Otamendi, Buenos Aires Province (Argentina), on an island of the delta of the Parana river (Fig. 1). A period of three years was necessary to collect these specimens, considering the fact that they are very rare to find. Skin and skull vouchers of the studied specimens were catalogued in the collection of mammals of the Mar del Plata Municipal Natural History Museum.

Cytogenetic analysis was based on mitotic metaphase chromosomes from bone marrow of animals previously injected with yeast (Lee and Elder 1980). Standard karyotypes were stained with Giemsa and C-bands were performed according to Hsu (1974).

The karyotype of *Bibimys torresi* shows a diploid number of $2n = 70$ and $AN = 76$. This karyotype comprises 30 pairs of acrocentric autosomes: one medium sized and the remaining small sized, and four pairs of small metacentric autosomes. The X and Y are small sized submetacentric chromosomes (Levan et al. 1964) (Fig. 2, top). The C-band pattern performed in the females, shows a faint centromeric heterochromatic band in the X chromosome, whereas in the autosomes heterochromatin is absent except in pair 3 which presents a very faint intercallary C-positive band (Fig. 2, bottom).

It is noteworthy that *Bibimys torresi* and *Scapteromys* species display a similar C-banded pattern, characterized by low amounts of heterochromatin, compared with that of other species of South American cricetid genera. This pattern was explained by a reduction in the amount of satellite DNA (Brum-Zorrilla et al. 1986; Freitas et al. 1984).

The available cytogenetic data show that *Scapteromys* species karyotypes range from $2n = 24$ to $2n = 36$ (Brum-Zorrilla et al. 1986; Freitas et al. 1984), whereas *Bibimys torresi* presents a markedly high chromosomal number. In this respect, previous reports suggest that in other South American cricetid-related lineages there are evidences of a directional trend towards a reduction in the chromosomal number, in the course of chromosomal evolution. Therefore, the higher diploid numbers within a lineage may represent the most primitive condition (Gardner and Patton 1976). Hence, if the reductional trend existent in other cricetid lineages counts also for the Scapteromyini, then *Bibimys* would represent an ancestral form of this group.

However, the karyotypes of *Bibimys* and *Scapteromys* differ so much in their diploid number (2n) and autosomal number (AN), that it is not possible to establish a comparison between them. The feasibility of obtaining G-bands in karyotypes of *Bibimys* would help to determine homologies and rearrangements with other Scapteronyini species.

Acknowledgements

We dedicate this paper to the memory of Dr. O. A. Reig without whom this work would not have been feasible. We thank Dr. Estela Bonaventura for providing the animals employed in this study, and Dr. E. Massoia for his helpful comments. This research has been partially funded by CONICET (grant PID No 3085300), to O. A. Reig and UBACYT (grant No EX228), to M. Mudry.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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MITTEILUNGEN DER GESELLSCHAFT

73. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde vom 26.–30. September 1999 in Bad Dürkheim

Einladung

Auf Einladung des Direktors des Pfalz-Museums für Naturkunde, Herrn Dr. Reinhard Flösser, findet die 73. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde von Sonntag, dem 26. September bis Donnerstag, dem 30. September 1999 im Pfalzmuseum für Naturkunde in Bad Dürkheim statt.

Vorläufiges Programm

Sonntag, 26. September:	Anreise
	ab 16.00 Uhr: Vorstandssitzung
	ab 19.00 Uhr: Zwangloser Begrüßungsabend
Montag, 27. September:	9.00 Uhr: Begrüßung
	9.30 Uhr: Hauptvortrag und Kurzreferate zum Themenschwerpunkt „Wildbiologie“
	14.00 Uhr: Posterdemonstration
	15.00 Uhr: Kurzvorträge
	16.00 Uhr: Mitgliederversammlung
	abends: Empfang durch die Stadt Bad Dürkheim
Dienstag, 28. September:	9.00 Uhr: Hauptvortrag und Kurzreferate zum Themenschwerpunkt „Sinnesphysiologie“
	14.00 Uhr: Posterdemonstration
	15.00 Uhr: Kurzvorträge
	Geselliger Abend
Mittwoch, 29. September:	9.00 Uhr: Hauptvortrag und Kurzreferate zum Themenschwerpunkt „Ökologie und Verhalten der Rodentia“
	14.00 Uhr: Posterdemonstration
	15.00 Uhr: Kurzvorträge
	18.00 Uhr: Posterprämierung
Donnerstag, 30. September:	Exkursion

Alle Interessenten, Mitglieder und Nichtmitglieder, sind zu dieser Jahrestagung 1999 der Deutschen Gesellschaft für Säugetierkunde in Bad Dürkheim herzlich eingeladen. Kongreßsprachen werden Deutsch und Englisch sein. Das Programm mit der Vortragsfolge wird den Mitgliedern – auf Anforderung auch Nichtmitgliedern – rechtzeitig vor der Tagung zugesandt. Sollten Sie eine persönliche Einladung benötigen, so wenden Sie sich bitte direkt an den 1. Vorsitzenden der Deutschen Gesellschaft für Säugetierkunde, Prof. Dr. H. Erkert, Zoologisches Institut, Morgenstelle 28, D-72076 Tübingen (Tel. 0 70 71/2 97 29 58; Fax-Nr. 0 70 71/29 46 34).

Wir bitten um die Anmeldung von Tagungsbeiträgen. Außer Beiträgen zu den genannten Themenschwerpunkten werden auch dieses Mal wieder verstärkt Kurzvorträge und Posterdemonstrationen zu anderen Fachgebieten der Säugetierkunde berücksichtigt.

Bitte melden Sie Kurzvorträge (15 min + 5 min Diskussion) sowie Posterdemonstrationen möglichst frühzeitig, spätestens jedoch bis zum 30. April (Ausschlußfrist) beim Geschäftsführer der DGS, Prof. Dr. R. Schröpfer, Fachbereich Biologie/Chemie, Barbarastr. 11, D-49069 Osnabrück (Tel. 05 41/9 69-28 48, Fax: 05 41/9 69-28 62) an. Der Anmeldung ist eine maximal einseitige informative Kurzfassung (Abstracts) (1,5-zeilig) beizufügen. Aus ihr sollen die Fragestellung, Methoden, Ergebnisse und die daraus gezogenen Schlußfolgerungen hervorgehen. Alle angenommenen Kurzfassungen werden wieder in einem Sonderheft der Zeitschrift für Säugetierkunde publiziert. Sie sind nach folgendem Schema abzufassen: Deutscher Titel, Leerzeile, englische Titelübersetzung (kleine Anfangsbuchstaben im Text; bitte ggf. einen „native speaker" konsultieren!), Leerzeile, Initialen und Familienname(n) des/der Autors(in) bzw. der Autoren(innen) in Großbuchstaben, Adresse, Leerzeile, Text. Aus arbeitsökonomischen Gründen bitten wir dringend darum, zusätzlich zum ausgedruckten Abstract möglichst noch eine Fassung auf Diskette (5.25″ oder 3.5″, IBM-kompatibler DOS-PC) in Form eines Microsoft Word-, Word Perfect- (5.1 oder 6.0) oder ASCII-Files mitzuschicken. Bitte formatieren Sie diesen File nicht! Die Maße für Poster werden im Juli-Rundschreiben der DGS bekanntgegeben.

Mit Fragen zum Tagungsort und zur Organisation wenden Sie sich bitte an Herrn Dr. Reinhard Flösser, Direktor des Pfalzmuseums für Naturkunde, Hermann-Schäfer-Str. 17, D-67098 Bad Dürkheim, Tel. 0 63 22/94 13-22, Fax: 0 63 22/94 13-11.

III. International Symposium Semiaquatic Mammals and their Habitats May 25–27, 1999 in Osnabrück, Germany

The 3rd symposium will give the opportunity to present new observations on the biology, the conservation, and the habitats of semiaquatic mammals. We also look for presentations that deal especially with the problem of structure and species diversity of inland-bank-ecotones regarding the presence of semiaquatic mammals.

A separate volume with abstracts will be printed, and it is planned to publish the contributions to the symposium.

Two round-table discussions will take place. One regarding the situation of the beaver in the European agricultural landscape and the other concerning the situation of the European mink.

An excursion to lakes and water courses will be organized.

For registration and further information contact: Prof. Dr. Rüdiger Schröpfer, Universität Osnabrück, FB Biologie/Chemie: Ethologie, Barbarastr. 11, D-49069 Osnabrück.
Tel. +49/(0)5 41/9 69-28 47, Fax +49/(0)5 41/9 69-28 62, e-mail: schroepfer@biologie.uni-osnabrueck.de

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Einsendung und Annahme von Manuskripten: Ms. zur Veröffentlichung sind einzusenden an den 1. Schriftleiter: Herrn Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel. e-mail: dkruska@ifh.uni-kiel.de

Über die Annahme von Ms. zur Veröffentlichung wird gemäß Geschäftsordnung der Deutschen Gesellschaft für Säugetierkunde entschieden. Der Eingang von Ms. wird sofort bestätigt, und nach Erhalt der Gutachten werden die Autoren über die Entscheidung umgehend informiert.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



ISSN 0044-3468 · Z. Säugetierkunde · 64(1999)2 · S. 65-128 · April 1999

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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Time of activity of a female free-ranging Lynx (*Lynx lynx*) with young kittens in Slovenia

By ILKA REINHARDT and S. HALLE

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Receipt of Ms. 19. 05. 1998
Acceptance of Ms. 14. 12. 1998

Abstract

We investigated the activity behaviour and time-budget of a female free-ranging lynx (*Lynx lynx*) in Slovenia during the first five months of post-partum from June–October 1995. Activity was monitored by means of a radio-collar with activity sensor, employing continuous automatic recording and discontinuous time-sampling. A total of 1818 data hours was analysed with respect to the prey status, distinguishing between days with and without kill, and age of the kittens. On average the female was active for 8.5 h per 24-h day. Activity at twilight and during daytime was generally higher than during night. On days when the female hunted she was more active and more diurnal than on days when she had access to a kill. During the later post-partum mobile phase the female covered a considerably larger home range, was much more active, and showed higher twilight and daytime activity than during the earlier stationary phase. Movements to and from a kill occurred irregularly throughout the night during the stationary phase, while the whole family went to a kill around sunset and returned back around sunrise during the mobile phase. When a kill was available, the female spent on average 81 % of the 24-h day with her kittens, but only 63 % on days with no kill. Times of absence from the den did not increase during the stationary phase as the kittens grew older. Activity timing is interpreted as a highly differential temporal adaptation to meet various contrasting challenges, i. e., hunting, defence of kills against competitors, protection of young, and home range patrolling. Comparison with data from Switzerland suggest that habitat structure in addition is likely to shape lynx activity in different areas.

Key words: Eurasian lynx, activity, radiotelemetry, time budget, breeding

Introduction

Recently, the Eurasian lynx (*Lynx lynx*) appaers to be regaining parts of its former areas of distribution (see BREITENMOSER-WÜRSTEN et al. 1998) due to re-introduction and legal protection. In this connection it is particularly interesting to know to which extent the species is able to adapt its behaviour to different ecological conditions. Two important aspects in this regard are hunting activity and time budgets, since flexible responses to the environment are to be expected with these behavioural traits in particular. However, data on lynx activity behaviour are rather fragmentary. In general, the species is assumed to be primarily nocturnal and crepuscular (MATJUSCHKIN 1978; HEMMER 1993), although diurnal activity is also known to occur (HALLER and BREITENMOSER 1986).

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Even less information is available on the relation between activity and breeding. The female lynx restricts its movements to a small part of its home range during the early rearing period, as also known from other Felidae (Seidensticker 1977; Sunquist 1981; Schmidt et al. 1997). Restricted space use is likely to be reflected in the activity pattern because the daily time schedule is closely linked to spatial behaviour. However, a feasible ad-hoc assumption about the total activity level is not possible since a breeding female has to balance the requirements of food intake with the specific challenges of rearing kittens. Increased hunting effort due to limited use of space during the early stationary phase may cause higher activity, while the extended use of space during the later mobile phase may also account for this as well.

In general, predators are known to time their activity in accordance to the activity pattern of their prey (e.g. Ables 1969; Sunquist 1981; Ferguson et al. 1988; Beltran and Delibes 1994). However, when a lynx manages to kill a large prey like a roe deer, which is the main prey of the European lynx (Pulliainen 1981; Sostak and Bunevic 1986; Breitenmoser and Haller 1987; Jedrzejewski et al. 1993; Pulliainen et al. 1995), it may feed on it for up to one week (Reinhardt, pers. obs.). Having a kill or not can be supposed to affect the activity behaviour directly, with the assumption that the level of activity will be lower when the animal has a kill to feed on. Furthermore, also the temporal pattern of activity over the 24-h day may vary between days with and without kill, because time can be allocated to different types of activity depending on the short-term food supply. Almost nothing is known about this aspect of lynx behaviour.

In this study we present data on the activity and time budget of an intensively studied free-ranging female lynx in Slovenia during the first five post-partum months. In particular, we focus on the effect of prey status on temporal behaviour during two distinctive rearing periods.

Material and methods

Study area

The study was conducted in the Kocevska region in Southern Slovenia (45°35′ N, 45°20′ E). The 620 km^2 study area is part of the Dinara Mountain Range. Elevations range from 300 to 1300 m. The fine-scale relief is typical of high karst regions with numerous dolines, caves, boulder fields, and rock faces. Forest covers up to 90 % of the terrain with *Abieti-Fagetum-dinaricum* as the dominant forest community. The climate is temperate continental with annual precipitation from 1400 to 1800 mm. The average mean temperatures in January and July are –2.9 and 17.8 °C, respectively.

Potential larger prey species of lynx are red deer (*Cervus elaphus*; annual harvest quote of 2–3 animals/100 ha), roe deer (*Capreolus capreolus*; annual harvest 0.7/100 ha), and a few chamois (*Rupicapra rupicapra*). Species that may compete or otherwise interact with lynx include brown bear (*Ursus arctos*), wolf (*Canis lupus*), red fox (*Vulpes vulpes*), golden jackal (*Canis aureus*), wild cat (*Felis silvestris*), badger (*Meles meles*), wild boar (*Sus scrofa*; annual harvest 0.8/100 ha), and a variety of raptor species.

Activity reading

The lynx female was caught in a box-trap in April 1994. It was tranquillised with Zoletil 100 (Virbac, France, a mixture of Tiletamin and Zolazepam), ear-tagged, and fitted with a radio-collar equipped with a tip switch as activity sensor (Wagener, Germany). The tip switch caused the pulsing rate of the transmitted signal to alter between slow and fast, depending on collar position. In addition, signal strength varied due to changes in transmitter orientation relative to the lynx body, and relative to the receiver antenna. Since we were mainly interested in locomotor activity, lynx activity was indicated by changes in both signal strength and/or pulsing rate.

Activity was recorded in two different ways: Continuous recording was performed by means of an automatic recording station (B + R Ingenieurgesellschaft, Germany), which allowed determination of lynx activity for each single minute. In addition, discontinuous activity recording (time-sampling) was used when the lynx was outrunning the receiving area of the recording station. It was then followed by car, and radio signals were monitored every 5 th minute for 60 sec with a hand-held Yagi-antenna and a portable receiver. A sample was classified "active" when three or more signal changes occurred during one minute, while inactivity was indicated by a steady signal pulse. In this way we followed the "predominant activity sampling procedure" which is considered most accurate for temporal activity assessment (TYLOR 1979). Compatibility of the two methods of activity reading was tested by simultaneous automatic recording and time-sampling for 20 h, which revealed a high agreement of 96.7 %. To make both methods directly comparable in data analysis the tapes from continuous recording were time-sampled to simulate discontinuous activity recording.

The lynx gave birth to two kittens on the 1 June 1995 and was then followed during the first five months of rearing, i. e., from June until October 1995. During the first weeks after birth lynx kittens remain stationary at the den-site to which the female always returned from hunting (called "stationary phase" hereafter). During this time the recording station was kept near to the den-site, fitted with a directional antenna oriented towards the den. This allowed to record female activity near the den as well as times and length of den attendance. When lynx kittens have grown up to an age of seven to eight weeks, mother and young left the natal area and the kittens started accompany their mother (called "mobile phase" hereafter).

Data analysis

Lynx activity was analysed with respect to the overall level of activity, the activity distribution over the 24-h day, and the relative activity allocation to different light phases. Twilight was defined as 1 h before and after sunrise and sunset, respectively. The basic time unit was hours of the clock. The proportion of samples scored active during each hour yielded the percent activity per hour, with the restriction that only hours with at least six activity samples were regarded in the analysis. The activity level was measured as the average activity per hour, per day, or per light phase.

Relative diurnality and crepuscularity indices were employed to compare the activity allocation to light phases between periods with different levels of activity and with different day length. The diurnality index I_D (modified after HALLE 1995) reflects the proportion of diurnal as compared to nocturnal activity and was calculated by

$$I_D = \left[\frac{(\Sigma\ AD)/hD}{(\Sigma\ AD)/hD + (\Sigma\ AN)/hN}\right] \cdot 2 - 1$$

in which Σ AD and Σ AN are the times of activity summarised for day and night, respectively, and hD and hN are day length and night length, respectively. I_D is positive if diurnal activity prevails (maximum: +1 when exclusively diurnal) and negative when nocturnal activity prevails (minimum: –1 when exclusively nocturnal). The crepuscularity index I_C (modified after HALLE 1995) reflected the relative proportion of twilight activity as compared to the average activity over the 24-h day and was valued by

$$I_C = \log\left(\frac{(\Sigma\ AC)/\Sigma\ A}{4/24}\right)$$

where Σ AC is the time of activity during the hours of twilight (SR ± 1 h and SS ± 1 h) and Σ A is the total time of activity during an entire day. I_C is positive when activity during twilight is increased compared to the average activity, and negative when it is decreased.

Lynx activity behaviour was analysed for the total study period, the two rearing periods, and in relation to the prey status. For the latter all days of the field season (separated by midnight) were categorised according to prey status by locating the female several times a day using the methods of triangulation (or "homing in", WHITE and GARROT 1990). Locations where the lynx remained for an evening or night were searched for carcasses of prey killed by lynx the following day with a trained dog. Days were classified as "day with kill" if the kill was actually found, or if the lynx returned to the same place for several nights. If there was no indication of a kill, i. e., when the lynx changed its position considerably in successive nights, the status "day without kill" was given. When data where ambiguous, days were classified as "status unknown". Note that this classification, however, only ap-

plies to large ungulate prey and not to voles and other small prey items, which may be food resources as well (e. g. Pulliainen 1981; Jedrzejewski et al. 1993; Pulliainen et al. 1995).

Differences in activity distribution over the 24-h day were tested with the Kolmogorov-Smirnov-test. When testing for differences depending on prey status, data from days with unknown status were excluded. Wilcoxon-signed-rank-tests for related samples were used for comparisons between days with and without kill, and between the two rearing periods. In the same way we tested whether the female was more often absent from the den during the second half of the stationary phase than during the first. We used Kruskal-Wallis one-way analysis of variance for independent samples, adjusted by a Bonferroni procedure (c. f. Toutenbourg 1994), to test for differences among the average activity level at daytime, night-time, and twilight. All P-values are for two-tailed test.

Results

General activity pattern and prey status

The total base of activity data consisted of 1 818 data hours of which 1 275 h (70 %) were covered by automatic recording and 543 h (30 %) by time-sampling. Each hour of the clock (1:00–24:00) was represented by 59 to 95 data hours with an average of 11.1 activity samples per hour. For 1 490 h from 103 days the prey status was known, of which 824 h from 49 days were classified as "days with kill" and 666 h from 54 days as "days without kill".

On average, the lynx was active for 35.5 % ($N = 1\,818$, $SD = 32.18$, $SE = 0.75$) or 8.5 h of the 24-h day. Averaged over the entire study period the daily activity pattern revealed no significant deviation from an even distribution over the 24-h day ($N = 1\,818$, Kolmogorov-Smirnov, $z = 12.29$, $P < 0.001$). However, after splitting days into three distinct light phases, the overall level of activity differed significantly among them ($N = 1\,818$, Kruskal-Wallis, $df = 2$, $P = 0.001$), being highest during twilight, intermediate during daytime, and lowest during the night.

The lynx was more active on "days without kill" (45.7 %) than on „days with kill" (28.3 %; $N = 24$, Wilcoxon, $P < 0.001$). Twilight and diurnal activity always prevailed but particularly so on "days without kill" ($I_C = +0.12$, $I_D = +0.15$ as compared to $I_C = +0.03$, $I_D = +0.06$ on "days with kill"). This indicates predominant hunting during broad day light.

Rearing periods

During the stationary phase the lynx used only 8 km^2 of her home range as compared to 110 km^2 during the later mobile phase. Correspondingly, the female was significantly more active during the mobile phase (39 %) than during the stationary phase (29.7 %; $N = 24$, Wilcoxon, $P = 0.004$). This activity increase was above all caused by much higher day and twilight activity, whereas nocturnal activity decreased during the mobile phase, resulting in a substantial change in the daily activity pattern (Fig. 1). Activity distribution over the three light phases was fairly even during the stationary phase ($N = 683$, Kruskal-Wallis, $P = 0.241$), while the difference twilight > day > night was highly significant during the mobile phase ($N = 1\,135$, Kruskal-Wallis, $P < 0.001$; twilight vs. daytime: $N = 706$, $P < 0.001$; daytime vs. night: $N = 964$, $P < 0.001$). Accordingly, diurnality and crepuscularity indices were higher for the mobile phase ($I_D = +0.13$, $I_C = +0.13$) than for the stationary phase ($I_D = -0.04$, $I_C = -0.06$).

For the effect of prey status on activity behaviour (Fig. 2), only "days with kill" could be compared between the two rearing periods, because too few data from "days without kill" were available for the stationary phase. On "days with kill" the activity level was about 28.6 % during the stationary phase with an almost even distribution over all light

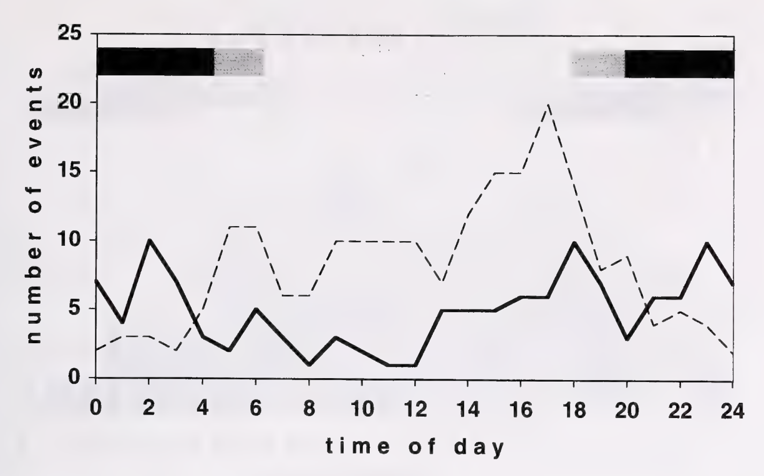
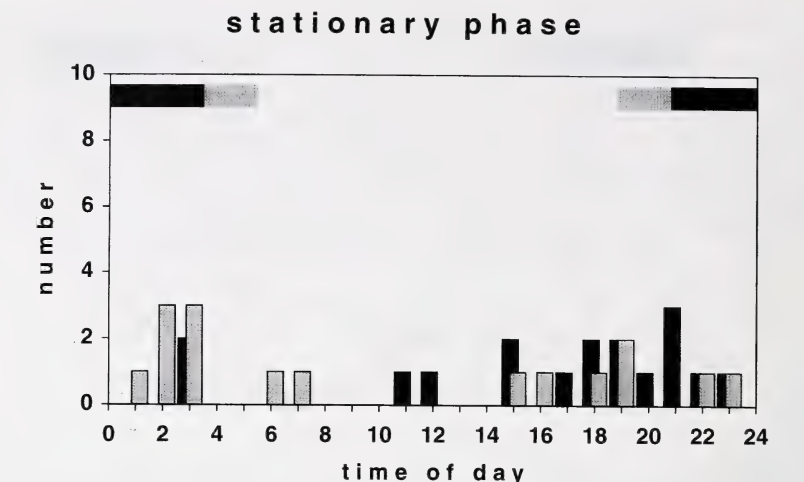


Fig. 1. Diel distribution of occasions when the lynx was recorded to move more than 500 m per hour. Solid line: stationary phase, broken line: mobile phase. The bars at the top indicate twilight and night-time hours.



Fig. 2. Mean values (± SE) of activity for each light phase (daytime, twilight, night-time), measured as the percentage of an hour with activity. Data are broken down to the two rearing periods and to the effect of prey status. For the stationary phase too few data were available for "days without kill" to include this category in the analysis.

conditions ($N = 344$, Kruskal-Wallis, $P = 0.188$; $I_D = -0.09$ and $I_C = +0.04$). The level of activity was almost the same during the mobile phase on "days with kill" (28.1 %), but now activity differed significantly among light phases ($N = 480$, Kruskal-Wallis, $P < 0.001$), decreasing in the order twilight > day > night (daytime vs. twilight: $N = 407$, $P < 0.001$; night vs. daytime: $N = 257$, $p = 0.003$; $I_D = +0.13$, $I_C = +0.19$). Crepuscular activity was by then about 1.6 times higher than the 24-h average.



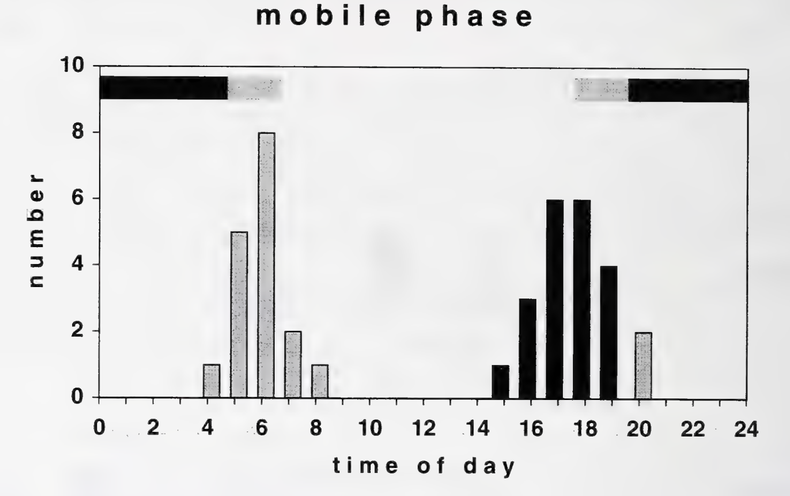


Fig. 3. Diel distribution of movements between the daytime location and the kill during the two rearing periods. Black bars: moving to the kill, shaded bars: returning from the kill. The bars at the top indicate twilight and night-time hours.

The reason for this difference in behavioural parameters became obvious when looking at the times when the lynx went to or returned from the kill (Fig. 3). As long as the kittens were stationary the female went to the kill and returned to the den at variable times. Later, when the kittens followed their mother, the pattern became much more regular, i. e., the family went to the kill in the evening and early night, and returned back to their resting place in the late night and early morning. During the mobile phase the level of female activity almost doubled on "days without kill" (51.5 %) as compared to "days with kill" (28.1 %). When she had no kill and was hunting, significantly more activity was performed during daytime and twilight than during the night (daytime vs. night: $N = 383$, $P < 0.001$; twilight vs. night: $N = 265$, $P < 0.001$; Fig. 4, c. f. Fig. 2).

To determine whether the female had preferred times for sleeping we computed the averages of the longest inactive period per hour of the day. The resultant 24-h pattern

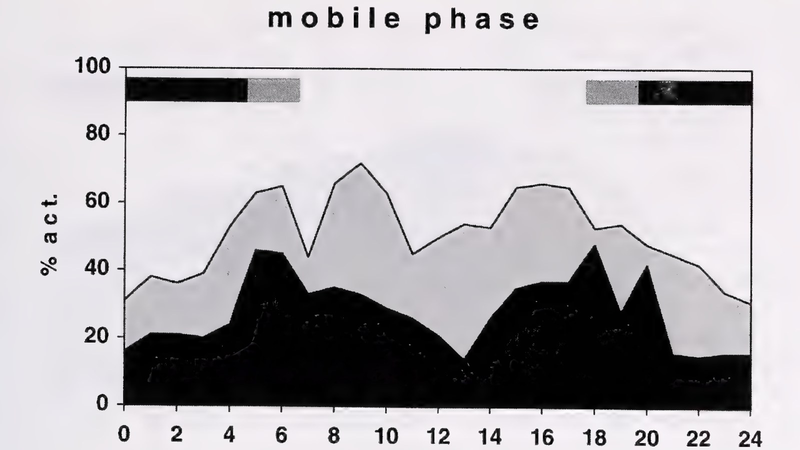


Fig. 4. Pattern of female activity at "days with kill" (black) and "days without kill" (shaded) during the mobile phase. The bars at the top indicate twilight and night-time hours.

was compared with the total distribution of inactivity (60 min. – X min. active/h) for the two rearing periods as well as for days with and without kill. The distributions always corresponded well with each other (N = 24, Spearman rank correlation, all $P < 0.001$, stationary phase: $r_S = 0.72$; mobile phase: $r_S = 0.92$; "days with kill": $r_S = 0.81$; "days without kill": $r_S = 0.86$), indicating that sleep was an integrated part of the main rhythm of activity and inactivity, respectively.

Den attendance

From 1 June the animal returned constantly to the same small area where she had her breeding den the previous year (Huber, unpubl. data). After a disturbance on 23 June the female moved to a second den, approximately 400 m up the slope, where two kittens aged about 4 weeks were found on 2 July. Also later during the stationary phase the lynx family repeatedly changed location a few hundred metres, so obviously the female had access to several auxilliary dens that where used alternatively. The female always returned to the place where she started from, so she probably was not accompanied by her kittens during the excursions. On 19 July the lynxes moved 3.5 km (straight line) to a place well outside the area where the female has been hunting during the previous seven weeks.

During the stationary phase the female spent on average 17.9 h of the day (74.5 %) near her kittens at the den. The time of presence, however, differed significantly between "days with kill" (80.6 %) and "days without kill" (62.6 %), being on average 4.5 h longer on "days with kill" (N = 24, Wilcoxon, $P < 0.001$). Relatively, presence at the den-site occurred more often during daytime on "days with kill" than on "days without kill" (N = 400, Mann-Whitney-U, $P < 0.001$, Fig. 5). However, differences in den attendance during night and twilight hours between "days with kill" and "days without kill" were not statistically significant (Mann-Whitney-U, night: N = 120, $P = 0.44$; twilight: N = 180, $P = 0.27$).

On "days with kill" the times of absence from the den corresponded generally well with the activity records (N = 24, Spearman rank correlation, $r_s = 0.71$, $P < 0.001$). However, activity during daytime was not closely related to the pattern of absence from the den, indicating high activity in the close vicinity of the den, probably performed as play

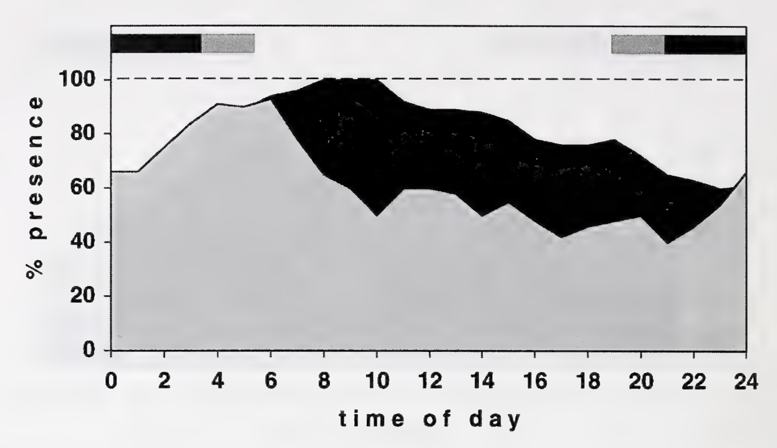


Fig. 5. Diel distribution of den attendance by the female at "days with kill" (black) and "days without kill" (shaded) during the stationary phase. The bars at the top indicate twilight and night-time hours.

and comfort behaviour. The time of absence from the den did not increase as the kittens grew older, instead it decreased slightly from 28 % to 24 % of the day (N = 24, Wilcoxon, P = 0.24).

Discussion

We are well aware that the data presented here are restricted to only one individual, hence the important aspect of behavioural variation among individuals had to be ignored. However, since there is only scarce information about the activity and early maternal phase of free-ranging Eurasian lynx, we feel that our approach to focus on one breeding female and to follow her closely through a whole summer may be justified.

According to the lumped data from the entire study period, activity appeared initially to be acyclic. However, a more detailed scrutiny of the data revealed a highly differentiated activity behaviour, in which prey status and rearing period had substantial effects on the pattern. In fact, our analysis verified that the flexible pattern of the females activity allowed for short-term adaptive responses to her and her kittens requirements.

The highest activity of the female was recorded during twilight and daytime, which is in accordance with a short survey of re-introduced lynxes in Austria (FESTETICS 1981). In contrast, MATJUSCHKIN (1978) observed the lynx in Russia to be mostly or predominantly nocturnal with only little diurnal activity. The general activity level of about 36 % in our study was considerably lower than the 58 % ALDAMA et al. (1991) reported for the Iberian lynx (*L. pardinus*). In particular, the lynx was less active on "days with kill" than on "days without kill", so obviously a lynx that already has a kill can lower its hunting effort and, as a rule, does not move over greater distances.

Behaviour during the stationary phase

The level of activity was almost the same on "days with kill" during the two rearing periods, portraying the basic activity level of a female lynx with cubs. During the stationary phase the lynx fed mostly at night, and also movements between den-site and kill occurred predominantly at night. This resulted in higher nocturnal activity on "days with kill" as compared to the mobile phase.

Time of absence from the den-site per day did not gradually increase with age of the kittens. This contradicts the assumption that the restricted hunting area during the stationary phase will demand increasing hunting efforts as kittens grow older and need more food, which in turn would lead to shorter den attendance and higher activity. So probably, the area close to the den-sites was a hunting ground sufficient to cover food demands during the entire stationary phase. This assumption is reasonable, since the large fields of dolines offer rich grazing for roe deer, while a stalking predator benefits from good cover.

This estimate of habitat quality, however, raises the question why behaviour at all changes during the transition to the mobile phase, if not for limited food supply. A suitable explanation may be a need for home range patrolling. Home range occupation was reported by Sunquist (1981) for a tigress while the activity of the former resident female was restricted to a small area during the early rearing period. The same resulted for lynx in Switzerland Breitenmoser et al., 1993). Hence, staying with the kittens too long may result in a loss of the home range, while starting to move with the kittens too early may endanger the kittens life. An observation made one week before the female moved with her kittens a longer distance for the first time may point to this difficult trade-off. The lynx made a remarkably extensive excursion over 15 h to the northern end of her range, and almost the same way was then taken accompanied by the kittens when they left the natal area. Thus, the mother most probably pre-explored the travelling route before.

Another reason for giving up the stationary phase may be due to energy constraints. The energy costs of lactation are high and exceed all other reproductive costs in eutherian mammals (Loudon 1985). Deag et al. (1987) proved that nursing cats (*Felis domestica*) lost weight at an increasing rate over the first eight weeks after parturition. Increasing costs of lactation may, therefore, demand to provide the kittens with solid food. To our knowledge there is no report of lynx carrying large prey or parts of it back to the den, and felids are not able to regurgitate food to their offspring as known from canids. Instead, they lead their young to the kill, resulting in the vagabond behaviour of the mobile phase.

Behaviour during the mobile phase

Activity behaviour during the mobile phase was bimodal (Aschoff 1957), and daytime was the preferred activity period irrespective of prey status. When the female had a kill, she went there together with her kittens in the evening, spent the whole night close to the kill, and left in the morning. Accordingly, the highest locomotor activity was recorded during twilight in this situation. This pattern may reflect a temporal adaptation to protect the kill against potential scavengers. Jedrzewski et al. (1993) found eight species of scavengers feeding on lynx kills in Poland, with wild boar having the greatest impact. In our study area the brown bear is probably an important competitor, which is mainly nocturnal (Kaczensky pers. comm.). It may be advantageous to stay near the kill at night to secure that the pay-back from time and energy investment is not taken away by another species. Against visually orientated diurnal scavengers like raptors blinding with leaves and branches was an efficient technique.

Even on “days with kill” activity was higher during daytime than during the night, suggesting that play and comfort behaviour mainly occurred during daytime. The activity rhythm of the kittens may thus partly explain diurnal activity of the female. Many mammalian species exhibit diurnal behaviour as juveniles and shift to nocturnality as adults, which is, for instance, known for Iberian lynx (Beltran and Delibes 1994), wild boar (Briederman 1971), and badger (Eibl-Eibelsfeldt 1954, cited in Aschoff 1957). If kitten activity would be a decisive factor, increased diurnality should exclusively be shown by females with young offspring.

After having consumed a kill completely, the female normally moved with her kittens during broad daylight to another area before hunting. Hunting times of the lynx were very variable during the mobile phase, but as a general rule tended to be higher during twilight and daytime. In the Swiss Jura Mountains, however, nocturnal and twilight activity prevailed distinctively (Bernhart pers. comm.). The different temporal hunting patterns in Slovenia and Switzerland may reflect adaptations to hunting on roe deer, the main prey of lynx in both areas (Breitenmoser et al. 1993; Huber unpubl. data) in differently structured habitats. In Slovenia, forest covers more than 90 % of the study area, so that deer can stay under cover for long periods of time. In this situation temporally flexible roaming may give the best hunting success. In the Swiss study area, however, forest cover is only about 39 % (Bernhart pers. comm.) and roe deer emerge predominantly in the evening to browse on pastures. Accordingly, lynx hunt especially along the forest edges during the evening and night (Breitenmoser and Haller 1987) with frequent indications of ambushing (Kaczensky pers. comm.). Since founders of both populations stem from the same population of origin in Slovakia (Haller and Breitenmoser 1986; Cop and Frkovic 1998), behavioural differences between Swiss and Slovenian lynx are likely to reflect responses to the two areas rather than individual or genetic variance. This indicates that behavioural flexibility of Eurasian lynx allows to adapt foraging to different ecological situations.

Acknowledgements

We gratefully thank P. Kaczensky and T. Huber for support and critical discussion, and J. Dieberger from the Institut für Wildbiologie und Jagdwirtschaft at Vienna as well as J. Stanisa for technical support. We also want to thank R. Müller and D. Wirz for assistance with data analysis and K. Hindenlang and two anonymous referees for their constructive comments. Funding was provided by the Austrian Federal Ministry of Science and Research (G.Z. 30.435/-23/92).

Zusammenfassung

Aktivität eines Luchsweibchens (Lynx lynx) während der Jungenaufzucht in Slowenien

Aktivitätsverhalten und Zeitbudget eines Luchsweibchens (*Lynx lynx* L.) in Slowenien wurden während der ersten fünf Monate der Jungenaufzucht von Juni–Oktober 1995 mittels Radiotelemetrie untersucht. Die Aktivität wurde teils kontinuierlich mit einer automatischen Registrierstation, teils diskontinuierlich durch “time-sampling” aufgenommen. Insgesamt wurden 1 818 Datenstunden hinsichtlich des Alters der Jungen analysiert, wobei zwischen Tagen mit und ohne Riß unterschieden wurde. Im Durchschnitt war die Luchsin pro 24 Std.-Tag für 8,5 Std. aktiv, wobei die meiste Aktivität in der Dämmerung und tagsüber erfolgte. An Tagen ohne Riß war sie stärker diurnal und insgesamt deutlich aktiver als an Tagen mit Riß. Verglichen zur frühen, stationären Phase der Jungenaufzucht, in der die Luchsin die Jagdausflüge auf einen kleinen Teil ihres Streifgebietes beschränkte, war sowohl die Gesamtaktivität als auch die Dämmerungs- und Tagaktivität in der späteren, mobilen Phase höher. Ortswechsel zwischen Riß und Tagesstandort erfolgten in der stationären Phase unregelmäßig über die Nacht verteilt, während Ortswechsel in der mobilen Phase sehr regelmäßig in der Morgen- bzw. Abenddämmerung stattfanden. An Tagen mit Riß verbrachte die Luchsin durchschnittlich 81 % des Tages bei ihren Jungen, jedoch nur 63 % an Tagen ohne Riß. Die Zeit der Abwesenheit von der Wurfhöhle nahm während der stationären Phase nicht mit dem Alter der Jungen zu. Die Verhaltensänderungen während der Jungenaufzucht können vor dem Hintergrund gegensätzlicher Erfordernisse (Jagd, Rißverteidigung gegen Konkurrenten, Schutz der Jungen, Streifgebietskontrolle) interpretiert werden. Ein Vergleich der Ergebnisse mit Studien aus Gebieten unterschiedlicher Habitatstruktur läßt darauf schließen, daß das flexible Jagd- und Aktivitätsverhalten des europäischen Luchses eine Anpassung an verschiedenartige ökologische Bedingungen erlaubt.

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Z. Säugetierkunde **64** (1999) 76–84

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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Aspects of mother-kid behavior in Alpine chamois, *Rupicapra rupicapra rupicapra*

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Receipt of Ms. 02. 10. 1998
Acceptance of Ms. 14. 01. 1999

Abstract

We studied mother-kid associations for 9 mother-kid pairs of alpine chamois (*Rupicapra rupicapra rupicapra*) from May to October 1991. Mother-kid distance was studied from birth to weaning of the young. We further investigated the spatial relationship between the kid and the closest alien chamois within a group throughout the 6 months. The synchronization of activities between the mother and her kid was also analyzed. When mother and kid were in the same group, they were next neighbors in 90 % of all observations. Mother and kid were closest to each other when lying, while they were furthest apart when mothers were grazing and kids lying. Mothers and kids spent most of their daytime in the same group. The synchronization of activities between the mother and her kid increased with increasing age of the young. Mother and kid maintained close contact throughout weaning. The close association of mother and kid throughout the first 6 months of life of the young likely evolved as an anti-predator behavior and is first maintained through suckling and later through synchronization of activities between mother and kid.

Key words: *Rupicapra*, mother-kid bond, ontogeny, synchronization

Introduction

Suckling behavior and particularly mother-young interactions such as synchronization of activities and maintenance of proximity are central for the development and survival of young ungulates, especially in the first few week after birth (EPSMARK 1971; GEIST 1971; SHACKLETON and HAYWOOD 1985). Although lactation is the most important care mothers give to their offspring in the first few months of their life, guidance, transmission of knowledge, and the learning of social behavior can further benefit the young (LENT 1974; RICHARD-HANSEN and CAMPAN 1992; RICHARD-HANSEN 1993). Especially during eagle (*Aquila chrysaetos*) attacks proximity to the mother or to a defending female can be crucial for chamois kids (KRÄMER 1969; LOCATI 1990). The time the young spend in the vicinity of their mother also seems to depend on the frequency with which they suckle (SHACKLETON et al. 1984; SHACKLETON and HAYWOOD 1985). As suckling frequency declines, the mother-kid bond may loosen as well. In Rocky Mountain bighorn sheep, *Ovis canadensis*, lambs spend less time with their mother and more time in the company of other lambs when they are weaned (BERGER 1979), although post-weaning mother-daughter associations occasionally occur at high population densities (L'HEUREUX et al. 1995).

Chamois kids belong to the 'follower' type (LENT 1974) and kids follow their mothers within a few hours of birth (COUTURIER 1938). Despite its evolutionary importance and ef-

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fects on social ontogeny and group structure, the development of mother-offspring bonds in ungulates has received little attention, apart from studies on suckling behavior (Robinson 1980; Clutton-Brock et al. 1982, 1989; Oftedal 1985; Festa-Bianchet 1988; White et al. 1989; Ruckstuhl and Ingold 1994; Hass 1995). Although mother-kid bonds seem to be the strongest associations in chamois, descriptions on the ontogeny and strength of these associations are rare (Krämer 1969; Richard-Hansen and Campan 1992; Richard-Hansen 1993). We do not know how proximity between mother and kid is maintained through ontogeny and how close mother-kid associations are compared to associations between the kid and an alien chamois.

The aim of this study was to obtain quantitative information on the ontogeny of spatial relationships and the synchronization of activities in mother-kid pairs. We further investigated the spatial relationship between kids and their closest neighbor, to evaluate the strength of the mother-kid bond in comparison to non-mother-kid associations.

Material and methods

Study area and animals

Nine individually marked female chamois and their kids were observed between May and October 1991, on the Augstmatthorn, Switzerland (see detailed description of the study site in Krämer 1969). The study area is in a game sanctuary where hunting is prohibited. Focal females were all tagged with yellow-colored plastic stripes glued around the horns. Kids were unmarked, but individually recognizable through pelage characteristics, scars, and size differences. Mothers were identified during suckles, as chamois only suckle their own offspring (Krämer 1969). Female home ranges were between 1 400 and 2 137 m above sealevel (Ingold and Marbacher 1991).

Date of birth was estimated to be mid-way between the last observation of a female without a kid and the first observation with a kid. One kid was born between June 3 and 12. The 8 other kids were born between May, 8 and 22. All observations were made from a point where most of the slope used by the focal females was visible. Observations were made with binoculars (10×40) and spotting scopes (30×60). Ages of females were estimated through counting of horn annuli at capture. The females ranged in age between 4 and 13 years (see Tab. 1).

Data collection

Each mother-kid pair was observed for 2 to 9 days, depending on presence and visibility. A total of 52 days (346 hours) focal scan sampling observations (Altmann 1974) were carried out. If several marked females were visible at the beginning of observation sessions, the female with the least observation hours or days was chosen as focal animal. Observations lasted between 2 and 14 hours (Tab. 1). Long observation hours (>8 hours) on the same mother-kid pair lasted usually from dawn to dusk, shorter observation periods (<8 hours) were distributed evenly throughout the day.

The activity (walking, standing, lying, or grazing) of the kid, the mother, and the kid's closest neighbor, as well as the distances between mother and kid and the kid and its closest neighbor were written down every 15 minutes. From these scan samples we calculated the percentage of time mother and kid were next neighbors, and the percentage of time an alien chamois and the kid were next neighbors. Focal observations shorter than 5 hours were discarded from the analysis, because short observation periods may not reflect average activity budgets or inter-individual distances of females and their kid (especially because sample sizes per female are relatively small).

Distances between individuals were estimated in animal lengths (referred to as chamois lengths). The next neighbor is defined as the adult chamois, which was closest to the kid at the moment of sampling. Animals were determined to be in the same group if they were closer than 50 chamois lengths from each other. Distances or proximity between mother and kid were estimated, when both were lying or grazing or, when the kid was lying and the mother was grazing. Distances between the kid and next neighbor were only estimated when both were grazing. Most chamois kids in our study area were weaned by November (Ruckstuhl and Ingold 1994). We therefore describe the ontogeny of the mother-kid relationship from birth throughout weaning.

Statistical analyses

Mean distances between mothers and kids were calculated separately for each mother-kid pair for the first 6 months of life of the kid. Differences in proximity between mother-kid and kid-next neighbor were tested with ANOVA (Sokal and Rohlf 1995). Differences in proximity were then tested each month using Mann-Whitney U-tests (Siegel and Castellan 1988) and Bonferroni adjusted significance levels. The effect of kid age (in months) and individual differences on the distances between mother-kid pairs were calculated using 2-way-ANOVA.

Some mother-kid pairs were sampled more than once per month. We therefore calculated the mean percent time mothers and kids had the same activity in a given month, to reduce pseudo-replication (Machlis et al. 1985; Leger and Didrichsons 1994). We calculated the percent time females and their kids had the same activity. Percentages were arcsine square-root transformed (Zar 1984). Medians are given with interquartile ranges, means are given with standard deviations.

Results

If mother and kid were in the same group, the kid was always closer to its mother than to any other adult throughout the first 6 months of life, except in September ($F = 41.33$, $df = 1$, $p < 0.001$; Fig. 1). Mother and kid were neighbors in 90 % of all observations throughout the summer (Fig. 2). When grazing, the kid always followed its mother. The distances between mother and kid were therefore small (Fig. 3 a). The apparent increase in distance between mother and kid from the 4th to the 6th month was due to individual differences ($F = 3.06$, $df = 8$, $p < 0.001$) in mother-kid pairs and was not age-related ($F = 0.63$, $df = 1$, $p = 0.44$).

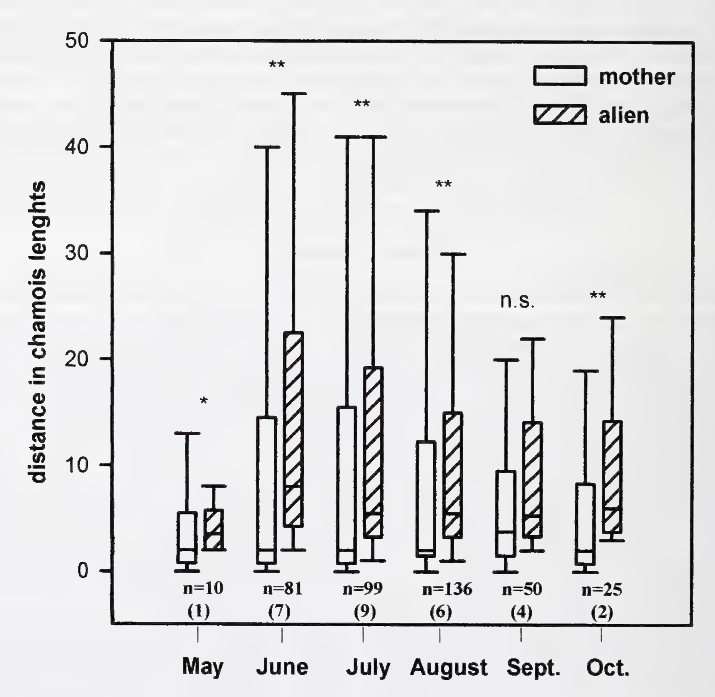


Fig. 1. Distances in chamois lengths between mother and kid, and between the kid and the next alien female from May to October 1991, Augstmatthorn, Switzerland. Number in brackets = number of mother-kid pairs, n = number of estimated distances. * = $p < 0.05$, ** = $p < 0.001$, n. s. = no significant difference (Mann-Whitney U-test, two-tailed). Box plots represent maxima, medians and minima with interquartile ranges.

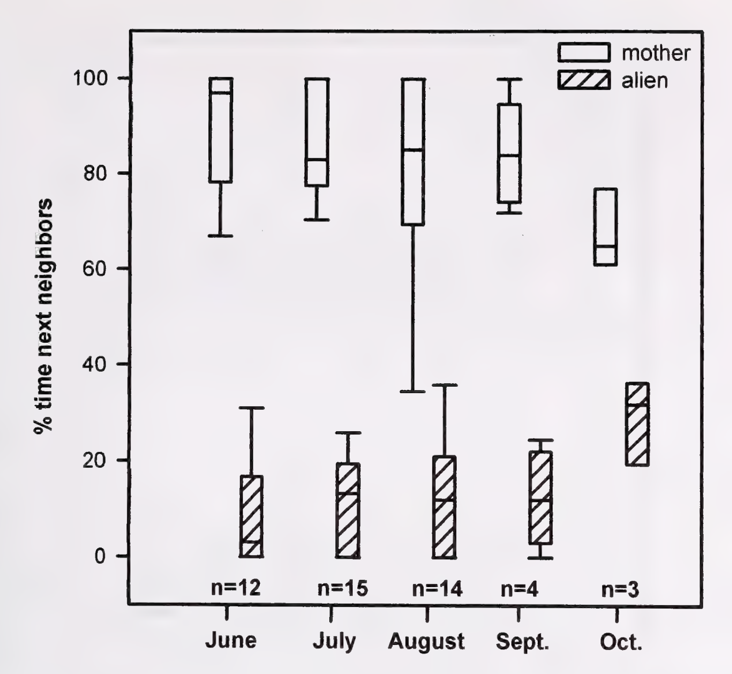


Fig. 2. Percent of observations when the next neighbor of a chamois kid was either its own mother or an alien female. n = observation days. Box plots represent maxima, medians and minima with interquartile ranges.

During the first 6 months of life of the kid mother and young most often lay in body contact with each other. The median distance therefore was often 0 chamois lengths (Fig. 3 b). In general it was the kid who actively searched body contact with its mother. Except in two observations the mother was the first to bed down and the kid then lay down beside her.

Adult females grazed for longer and more frequently than their kids. After a longer lying phase, but also when the mother was grazing, the kid often remained bedded. Therefore the mother automatically increased the distance between her and her young while grazing (Fig. 3 c). Hence greater distances were observed when the kid was lying and the mother grazing than when both had the same activity. As distances between mother and kid showed, they usually stayed in close proximity to each other when they were in the same group.

Mother and kid did not only spend most of their time in the same groups, but they also were closest to each other (Figs. 1 and 4). The percent time mother and kid spent in the same group during a day varied between and within mother-kid pairs (Tab. 1). While chamois number 4 was always seen in the same group as her kid during all observations (6 days), chamois number 6 was with her kid in less than 50 % of the observation period in 2 of 3 days. Longer periods of separation between mother and kid were rare but happened sometimes when mothers went to natural salt licks a few hundred meters from their preferred grazing grounds. Kids then stayed in the company of another mother and her kid. Separations between mother and kid could last up to 6 hours (2 observations). After a separation the mother always returned to the place where she had left her kid. If it was no longer there she started walking around in search of her kid often calling, and looking around. After the mother and kid reunited the kid attempted to suckle immediately.

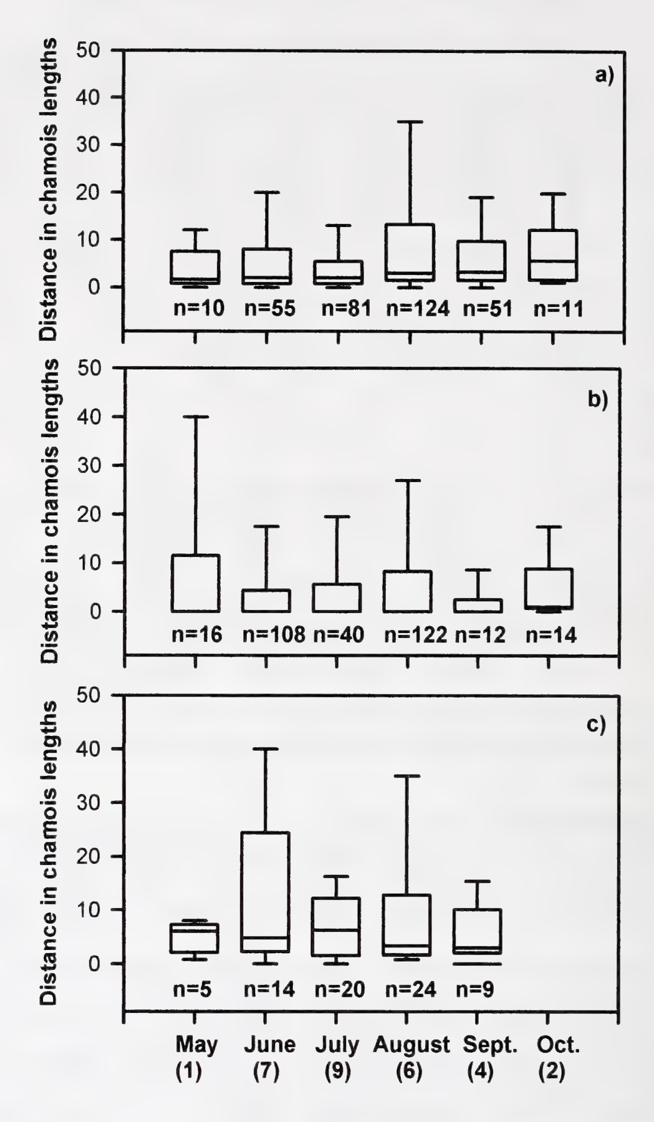


Fig. 3. Distances in lengths between chamois mother and kid when a) both were grazing or b) lying, and c) when the mother was grazing and the kid lying. n = number of estimated distances. Number in brackets = number of mother-kid pairs. Box plots represent maxima, medians and minima with inter-quartile ranges.

A kid's age affected the percentage of time mother and kid had the same activity ($F_{4,23} = 5.09$, $p < 0.005$). Mothers and kids were least synchronized in their activities in June (61 ± 16 % of observation time) and July (69 ± 8 %), more synchronized in August (78 ± 5 %) and September (78 ± 9 %) and most in October (86 ± 6 %; significant difference between June, July, and October: Scheffé post-hoc, $p < 0.05$). There were no individual differences in percent time spent in the same activity ($F_{5,22} = 0.85$, $p = 0.53$).

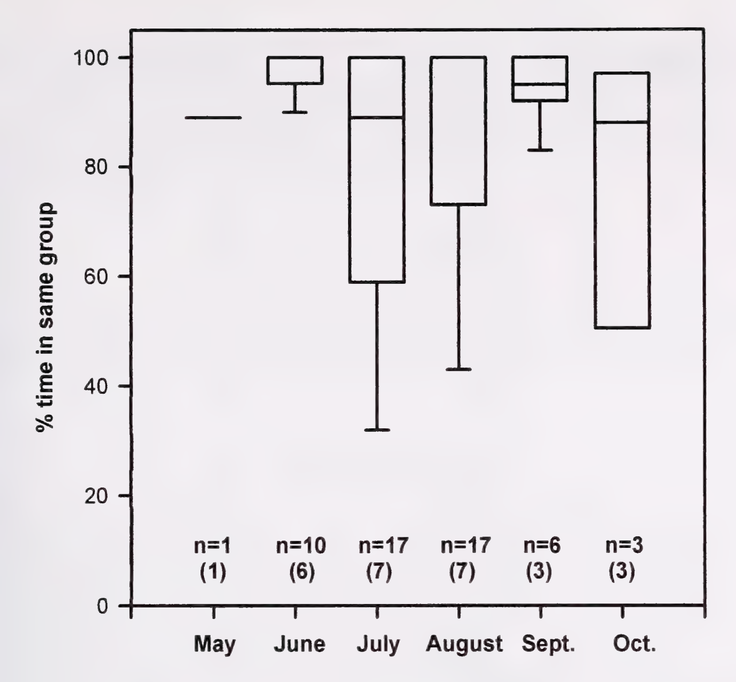


Fig. 4. Percent time chamois mothers and kids spent together in the same group during observations from May to October 1991, Augstmatthorn, Switzerland. n = observation days. Number in brackets = number of mother-kid pairs. Box plots represent maxima, medians and minima with interquartile ranges.

Discussion

Mother and kid maintained a very close proximity to each other in the first 6 months of the kid's life, as described for isard, *Rupicapra pyrenaica pyrenaica*, (RICHARD-HANSEN and CAMPAN 1992). They spent most of their time in the same group and were mostly next neighbors and therefore were closely associated. With increasing age the kid moved more freely within a group, probably in accordance with the increased time it spent grazing. The kid therefore sometimes was in the vicinity of an alien female, although it stayed most often close to its mother. The chamois is a follower type and the mother defends her kid against predators instead of relying on concealment as in the hiding types (LENT 1974). It is therefore important for the mother and her kid to stay in close proximity to each other (KRÄMER 1969). Suckling further increases the benefit to the young and maintains the strong bond between mother and offspring. Chamois often live in rugged terrain and the kid probably also depends on guidance through difficult terrain (KRÄMER 1969; GEIST 1971).

Kids did not graze often in their first month of life and usually fed close to their mothers, decreasing the average mother-offspring distance. Interestingly, the distance between mother and kid on average was always shorter than the distance between the kid and an alien chamois, as suggested by PACHLATKO and NIEVERGELT (1987). This is contrary to what we would expect if the process of weaning weakened the mother-offspring bond (GEIST 1971). When mother and kid were separated the kid was never alone, but was with other kids in a 'kindergarten' or in the company of a 'baby-sitter' (RUCKSTUHL and INGOLD 1998). This might explain why kids on average are less than 10 animal lengths

Table 1. Percent time mother-kid pairs spent in the same group during observation hours, at the Augstmatthorn, Switzerland, 1991. Age = estimated age of the mother. % in same group = percent of the total observation time/day, when mother and kid were together in the same group.

Mother #	Age	Observation day	Observation hours	% in same group
1	5	July 7	5.5	91
1	5	August 4	5	100
2	5	August 3	10.5	52
2	5	September 19	5.25	100
2	5	October 3	5.25	100
3	13	June 26	9	97
3	13	August 12	6.25	100
3	13	August 20	8.5	100
3	13	September 16	10.25	95
4	8	July 1	5	100
4	8	July 2	7.25	100
4	8	July 28	9.25	100
4	8	July 30	7.25	100
4	8	August 15	9.5	100
4	8	August 22	5.5	100
5	8	July 11	5.25	100
5	8	July 20	6	83
5	8	August 7	9.5	37
5	8	August 13	11	73
5	8	August 27	13.5	93
5	8	September 20	6.5	69
6	11	August 14	7.75	84
6	11	August 21	7.5	43
6	11	October 10	10.25	39
7	5	June 11	8.25	88
7	5	July 20	8	69
7	5	August 5	6.75	100
7	5	August 22	8.25	100
8	8	July 30	5	85
8	8	August 16	9	96
8	8	October 4	8	100
9	7	June 22	8.5	97
9	7	July 23	7.5	100
9	7	July 30	8	69
9	7	August 13	7	64
9	7	August 16	6.25	96
9	7	October 11	9	89

away from the next alien chamois within their group. As suggested by RICHARD-HANSEN (1993) kids seem to be attracted by peers and often also approach adult females. Adult females often respond to such an approach by threatening with their horns or attacking (LOCATI 1990), leading to the greater observed distances between the kid and alien females compared to the kid with its own mother.

Synchronization of activity is crucial for group cohesion (JARMAN 1974; BENHAM 1982; ROOK and PENNING 1991; AGESUMA 1995). Mothers and kids were least synchronized in their activities (grazing/lying) in June and July and most synchronized in October. In the first few weeks kids do not spend much time grazing and mainly depend on their mothers' milk. As the kids grow older they increase the time spent grazing and therefore likely become more synchronized with their mothers. On the other hand kids suckle less often and for shorter periods in September and October (RUCKSTUHL and INGOLD 1994),

and the mother-kid bond could consequently decrease. Nevertheless, we observed a strong mother-kid bond in our study area throughout the season; which may have two different reasons: 1) in the first few months of life, the kid depends on the mother's milk and it therefore should have a strong incentive to stay close to its mother, 2) as the mother-young bond loosens up because of weaning, proximity may be maintained through increased synchronization of activities.

Acknowledgement

This study was financed through the Federal Game Department and the Game Department of the Canton of Berne. We are thankful to M. Festa-Bianchet and P. Neuhaus and an anonymous referee for comments on an earlier draft of this manuscript.

Zusammenfassung

Aspekte der Mutter-Kindbeziehung bei der Alpengemse (Rupicapra rupicapra rupicapra)

Am Augstmatthorn im Berner Oberland, Schweiz, wurde vom Mai bis Oktober 1991 die Mutter-Kind Beziehung von Gemsen (*Rupicapra rupicapra rupicapra*) untersucht. Wenn Mutter und Kind in derselben Gruppe waren, so waren sie meistens nächste Nachbarn (außer im September) und verbrachten die meiste Zeit nahe beisammen. Die Aufrechterhaltung der Nähe schien von dem Kitz aus zu kommen. Die größten Distanzen zwischen Geiß und Kitz wurden gemessen, wenn die Geiß äste und das Kitz lag. Obwohl die Kitze mit zunehmendem Alter unabhängiger wurden, blieb die enge räumliche Beziehung bestehen. Mit zunehmendem Alter der Kitze waren Mutter und Kind in ihren Aktivitäten stärker synchron.

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Z. Säugetierkunde **64** (1999) 85–90
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Estimating porcupine (*Erethizon dorsatum* Linnaeus, 1758) density using radiotelemetry and replicated mark-resight techniques

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Receipt of Ms. 31. 07. 1998
Acceptance of Ms. 15. 10. 1998

Abstract

Quantitative estimates of the density of North American porcupines (*Erethizon dorsatum* Linnaeus, 1758) were obtained in two adjacent study areas in central Massachusetts (northeastern U.S.). Using mark-resight (with radio-marked porcupines) estimators with data collected on one single and four replicated surveys, none of the estimates (range = 10–42 porcupines/km^2) provided the relative precision needed to detect area-specific differences in density. This was because of the small samples of marked individuals (range= 5–12/survey; 4–6/km^2), low observability of porcupines during surveys ($\bar{x}$ = 15% of marked animals seen; range = 0–40%), and low numbers of surveys. Porcupines are more reclusive than we previously thought, and intensive survey efforts are needed to obtain reasonably precise density estimates in forested habitats.

Key words: *Erethizon dorsatum*, porcupine, mark-recapture, density estimation

Introduction

Despite the apparent abundance and wide geographic distribution of the porcupine in North America, there exist few quantitative estimates of population density for this species. In addition to helping make sense of demographic data, such estimates are useful for interpreting the role of porcupines in a forest ecosystem (e.g. Krefting et al. 1962; Keith and Cary 1991) or gauging the effectiveness of an eradication program (e.g., Dodge 1959; Brander and Books 1973).

We wanted estimates of porcupine population density for use in demographic (Hale and Fuller 1996) and habitat (Griesemer et al. 1995, 1996, 1998) studies we were conducting in central Massachusetts. Censuses using tracks in snow have been used in a number of studies (e.g., Curtis 1944; Brander 1973; Powell and Brander 1977; Smith 1977; Roze 1984), but when we followed tracks in snow we often encountered networks of intersecting and overlapping porcupine trails in concentrated denning areas where porcupines shared feeding trees and/or dens (Griesemer et al. 1996). This precluded our successful use of this technique.

Other methods besides censuses have been employed to estimate porcupine numbers, but most reports seemed unsatisfactory or incomplete. Several researchers (Taylor 1935; Reeks 1942; Golley 1957; Krefting et al. 1962; Dodge 1967) based population estimates on the number of porcupines seen or shot over a time period. These counts may have provided minimum numbers, but did not account for missed animals or immigrants. Shapiro (1949) used line strip techniques but did not detail his methods, did not account for

0044-3468/99/64/02 – 085 $ 12.00/0

potential bias due to low sighting probability, and did not provide an estimate of standard error. BRANDER (1973) used mark-recapture methods to estimate porcupine numbers and to generate an estimate of standard error. His study, however, lacked evidence that assumptions of mark-recapture methods (e.g., a closed population, equal catchability, and no loss of marks) were not violated.

The mark-resight method (OTIS et al. 1978) described in this study was used in association with radio-marked animals (cf. MILLER et al. 1997) in an attempt to assess its relative precision and feasibility as applied to the study of porcupines. We present our results, discuss the shortcomings of our efforts, and suggest means by which porcupines might be more rigorously counted.

Study area

We sampled 2 survey areas on the Prescott Peninsula at the Quabbin Reservoir in central Massachusetts, an area covered by Transition Hardwoods-White Pine-Hemlock forest (WESTVELD et al. 1956). Elevation on the study areas ranged from 162 to 351 m and the terrain was hilly, including some areas with steep rocky slopes.

The East and Central survey areas covered 2.2–2.6 km^2 and 2.2–3.1 km^2 respectively, and were located about 1 km apart. The East area included a very steep rocky ridge where numerous porcupine dens were concentrated, and had significantly fewer white pines (*Pinus strobus*) than the Central area (GRIESEMER et al. 1996, 1998). The Central area was only moderately hilly and lacked rocky slopes. There were fewer den sites and usually they were hollow trees or logs. We established these survey areas to encompass porcupine winter and summer home ranges as determined from radio-tracking 50 different individuals from July 1991 to September 1993 (HALE and FULLER 1996); this allowed us to maximize the number of radio-marked porcupines in the areas at the time of the surveys.

Material and methods

Porcupines were captured by hand or in live traps by focusing efforts in two portions of the Prescott Peninsula that eventually became our study sites. Captured individuals were marked with 40-g radio-collars and small (3 mm × 10 mm) yellow plastic eartags (HALE et al. 1994; HALE and FULLER 1996). Some individuals also had one to three 1.5 × 1.5 cm pieces of colored vinyl taped affixed to the end of their 20-cm radio antennas, but we assumed that none of the marking devices were so conspicuous as to cause the initial sightability of marked animals to differ from that of unmarked ones (in fact, at least 4 marked porcupines were initially classified as unmarked by survey observers and only subsequently verified as marked by an independent observer with a telemetry receiver).

Data for the mark-resight estimates were collected concurrently during nine surveys carried out during spring and autumn 1992, and spring 1993. To maximize the sightability of porcupines, each survey was conducted during these parts of the year when most porcupines were out of dens and the forest canopy was relatively open (GRIESEMER et al. 1998). Of the nine surveys, two surveys were made in the East area during each of the three seasons. The remaining surveys were conducted in the Central area, once in fall 1992 and twice in spring 1993.

In each study area, we mapped twelve 1.5- to 3-km long parallel transects 100-m apart; the first transect line was begun at a random point no nearer than 50 m, and no farther than 100 m, from the survey area boundary. Each transect was walked in approximately 2 hours by solitary persons experienced in looking for porcupines or by pairs of less experienced persons (e.g., at a rate of about 1 km/h). Transects walked in a single day comprised one survey.

When a porcupine was sighted it was classified as marked or unmarked, based on observation with binoculars: The location of each sighted porcupine was marked with flagging. Immediately after the transects were completed, all radio-marked porcupines in or near the survey area were tracked and visually located to verify those reported as being seen from the transect lines, and to identify those in the survey area but not seen.

Mark-resight density estimates were calculated using NOREMARK (WHITE 1996) which calcu-

lated simple Lincoln-Petersen estimates for single surveys, and joint hypergeometric maximum-likelihood estimates (JHE) and 90% confidence intervals (CI) for user-specified alphas for replicated surveys (e.g., MILLER et al. 1997). To investigate the actual effort needed to identify differences between mark-resight estimates of porcupines, we identified several combinations of observability, marked animals available, and number of repeated surveys for a hypothetical population, and then estimated the population density using NOREMARK.

Because our porcupines were marked with radio-collars, we could monitor deaths and emigration and determine how many marked individuals were present on the survey area on each survey day; thus, we assumed our population was closed. Because these marked animals were previously captured opportunistically within the study area and monitored for up to 2 years, we recognize that our marked sample may not have been representative of the population either at the time of capture or at the time of the survey. However, because there is no feasible way to make such an evaluation, we assumed the sample was representative for the purposes of these analyses. We also recognize that a commonly violated assumption of mark-reobservation studies is that of "equal catchability", resulting in a negative bias in the estimate. In this study porcupines sighted in trees and on the ground might have unequal sighting probabilities. Population densities for each such sub-population, as well as for different ages and sexes, should ideally have been estimated separately, but the small sample size in this study ruled out this possibility. However, the different methods used for initial captures and later resights should cause any bias produced by unequal catchability to be relatively small. We found that the sighting location (ground or tree) was, in fact, independent of the marked/unmarked status of porcupines ($X^2 = 0.03$, d.f. = 1, P = 0.86).

Results

During each of the nine surveys, 2–10 porcupines ($\bar{x} = 6.4$) were seen by observers (Tab. 1); this comprised 4–32% ($\bar{x} = 16\%$) of the estimated population. Although 5–12 marked porcupines were available to be seen during each of the surveys ($\bar{x} = 7.2$; this comprised 5–27%, $\bar{x} = 18\%$ of the estimated population), only 0–2 of these were seen ($\bar{x} = 1.0$; $\bar{x}$ proportion seen = 0.15, range = 0.00–0.40). During the five area-specific survey periods, the minimum number of porcupines known to be alive (MNA) varied from 9–16. Point estimates of density determined by mark-resight methods varied 4-fold (range = 10–42/km^2) in the East area and by 1.5-fold (range = 11–17/km^2) in the Central area, but significant differences among seasons or areas could not be detected (Tab. 1).

Our simulations, given hypothetical population of 100, indicated that increasing the proportion of the population seen from 0.10 to 0.30 resulted in a 57% reduction in confidence interval length (Tab. 2). Similarly, increasing the proportion of the population marked from 0.20 to 0.40, or increasing sighting occasions from 2 to 4, resulted in 40 and 38% reductions, respectively. Improving all three parameters simultaneously resulted in an 83% reduction.

Discussion

Even with the major effort we expended in trying to enumerate porcupines, our quantitative estimates using the mark-resight method were unsatisfactory. Though our mark-resight density estimates for both sites and all surveys (10–42/porcupines/km^2) are comparable to other relatively recent estimates (5–18/km^2; POWELL and BRANDER 1977; ROZE 1984) from mixed forests, unrealistic variation among survey estimates make us reluctant to say much about differences in porcupine density. At the time of our surveys, we had no good feel for porcupine abundance, much less the proportion of animals marked or the likelihood of seeing animals while slowly walking through the woods. This, combined with the unavailability of good computer models to augment our efforts, resulted in imprecise, though probably not inaccurate, population estimates.

Table 1. Porcupine survey data and the resulting population density estimates in two study areas on the Prescott Peninsula in central Massachusetts as determined by using mark-resight estimators (and computer program NOREMARK; WHITE 1996).

Area	Date of survey	No. of marked porcupines available	No. of marked porcupines seen	Proportion of marked porcupines seen	No. of unmarked porcupines seen	Minimum no. known alive (MNA)	Popultion estimate	Size of survey area (km^2)	Density estimate	
									No./km^2 (90% CI)	MNA
East	29 Apr 92	5	1	0.20	4		17.0[a]			
	13 May 92	6	2	0.33	5		17.7			
						Total 11	22[b]	2.2	10 (6–25)	5
	17 Oct 92	6	0	0.00	10		76.0			
	31 Oct 92	9	1	0.11	6		39.0			
						Total 16	123	3.1	42 (13–354)	5
	28 Apr 93	5	2	0.40	6		17.0			
	5 May 93	5	0	0.00	9		59.0			
						Total 14	43	3.1	14 (7–52)	5
Central	24 Oct 92	6	1	0.17	3		16.5			
						Total 9	24	2.2	11 (5–84)	4
	1 May 93	12	1	0.08	1		18.5			
	8 May 93	11	1	0.09	5		41.0			
						Total 16	45	2.6	17 (9–64)	6

[a] Lincoln-Petersen estimate.
[b] Mark-resight population estimate for a closed population using joint-hypergeometric maximum-likelihood estimator.

Table 2. Variation in precision of mark-resight porcupine population estimates given a) different sightability, b) proportion of animals marked, c) number of repeated surveys, or a combination of all three. All estimated are based on a hypothetical population of 100 porcupines, and use joint hypergeometric maximum likelihood estimates (JHE) as calculated by the computer program NOREMARK (WHITE 1996).

	Sightability	Proportion of porcupines marked	Number of porcupines seen			No. of repeated surveys	Total (90%CI)
			Total	Marked	Unmarked		
a)	0.10	0.20	10	2	8	2	99 (57–235)
	0.30	0.20	30	6	24	2	99 (74–150)
b)	0.10	0.20	10	2	8	2	99 (57–235)
	0.10	0.40	10	4	6	2	99 (70–176)
c)	0.10	0.20	10	2	8	2	99 (57–235)
	0.10	0.20	10	2	8	4	99 (65–176)
all)	0.30	0.40	30	12	18	4	100 (87–117)

Our simulation modeling that incorporated realistic data supported the notion that the precision of mark-resight estimates can be improved by increasing the number of surveys, the number of marked porcupines, and/or the number of porcupines seen per survey (e.g., ROBSON and REGIER 1964; RICE and HARDER 1977; POLLOCK et al. 1990). From a practical point of view, increasing the number of sighting occasions and increasing the number of marked porcupines might be the best way to increase precision of estimates. Increased search effort might help, but we have no data to test this potential improvement.

Acknowledgements

We are grateful to S. GRIESEMER, D. BROWNLEE, E. YORK, S. KOT, M. BRADY, G. GARNETT, T. LEONARDO, E. HETRICK, S. HOKENSON, S. SCHALLER, L. SALAS, T. OLIVER, and numerous undergraduate students for field assistance. We received funding and support from the U. S. Department of Agriculture (USDA) Forest Service Northeastern Forest Experiment Station; a USDA McIntire-Stennis grant; the College of Food and Natural Resources and Department of Forestry and Wildlife Management at the University of Massachusetts, Amherst; the Metropolitan District Commission (especially P. LYONS); and the Massachusetts Cooperative Fish and Wildlife Research Unit, U. S. Fish and Wildlife Service (now Biological Resources Division of the U. S. Geological Survey). L. MACDONALD, G. SMITH, and 2 anonymous reviewers provided many helpful suggestions on an earlier draft of this study.

Zusammenfassung

Dichteschätzungen von Baumstachlern (Erethizon dorsatum Linnaeus, 1758) mittels Radiotelemetrie und Sichtungen markierter Individuen

Quantitative Schätzungen der Dichte von nordamerikanischen Baumstachlern (*Erethizon dorsatum* Linnaeus, 1758) wurden in zwei benachbarten Untersuchungsgebieten von Zentral-Massachusetts (nordöstl. USA) durchgeführt. Die Daten wurden hauptsächlich an markierten Tieren über Telemetrie und Sichtungen während einmaliger und wiederholter Kontrollgänge erhoben. Keine der Abschätzungen (10–42 Ind./km^2) lieferte eine hinreichende Genauigkeit, um Regionen-spezifische Unterschiede in der Dichte zu ermitteln. Gründe dafür könnten in der geringen Anzahl markierter Individuen liegen (5–12 Ind./Kontr.; 4–6 Ind./km^2), in der geringen Sichtung von Baumstachlern während der Kontrollgänge ($\bar{x}$ = 15% der markierten Individuen; Schwankung = 0–40%) und in der geringen Anzahl von Kontrollgängen. Baumstachler leben offenbar stärker zurückgezogen als angenommen. Intensivere Kontrollen sind notwendig, um präzise Daten über Dichteschätzungen in Waldhabitaten zu erhalten.

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Z. Säugetierkunde **64** (1999) 91–106

http://www.urbanfischer.de/journals/saeugetier



ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Chromosomal characterization and relationship between two new species of *Ctenomys* (Rodentia, Ctenomyidae) from northern Córdoba province, Argentina

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Receipt of Ms. 06. 03. 1998
Acceptance of Ms. 14. 10. 1998

Abstract

Karyotypes of two recently described species of *Ctenomys* from northern Córdoba province (Argentina) were studied. *C. osvaldoreigi* is only known from the type locality in the high valleys of the Sierras Grandes at more than 2000 m above sea level. The karyotype consists of 2n = 52 chromosomes with FN = 56 and includes 22 pairs of telocentric autosomes that decrease gradually in size, a pair of subtelocentric autosomes (n°8), two pairs of small metacentrics and a pair of sex chromosomes. Three populations from the northeastern plains of Córdoba province (including one from the type locality) of *C. rosendopascuali* were analyzed. All individuals were 2n = 52 but FNs of the three populations were different. Individuals from Los Mistoles showed FN = 62 and the karyotype consists of a large subtelocentric autosomal pair, a medium-sized subtelocentric (n°8), twenty telocentric and three small metacentric pairs plus a pair of sex chromosomes. Candelaria specimens had FN = 64; the karyotype includes a second large subtelocentric pair which replaces a large telocentric, the remainder of the complement being similar to Los Mistoles. A further large subtelocentric occurs in the Mar Chiquita population, thus FN = 66; the remainder of the karyotype does not differ from the two other populations. In order to compare the new species to a known species of the same general geographical area, four populations of *C. bergi* from northwestern Córdoba were karyotyped. All specimens had 2n = 48, FN = 90. The three karyotypes found in *C. rosendopascuali* are remarkably similar and obviously related to that of *C. osvaldoreigi* through relatively simple chromosomal rearrangements, which confirms their morphological and molecular proximity.

Key words: *Ctenomys rosendopascuali*, *C. osvaldoreigi*, *C. bergi*, northern Córdoba, karyotype

Introduction

The South American Octodontoidea are a remarkable group of mammals with respect to their extraordinary karyotypic diversity. Diploid chromosome numbers range from 2n = 10 in the Bolivian species *Ctenomys steinbachi* (Ctenomyidae) (Anderson et al. 1987; Ruedas et al. 1993) to 2n = 102 in *Tympanoctomys barrerae* (Octodontidae) (Contreras et al. 1990). Fundamental numbers (FN) also vary enormously (16–202). Most of this chromosomal diversity is due to karyotypic variation within a single genus: *Ctenomys* (Bidau et al. 1996; Contreras et al. 1990; Giménez et al. 1997; Ortells 1995; Ortells et al. 1990; Reig et al. 1990, 1992).

Ctenomys, with more than 60 extant species, is one of the best examples of "explosive" speciation accompanied by extensive karyotype repatterning (Bidau et al. 1996;

0044-3468/99/64/02-091 $12.00/0

REIG 1984, 1989; REIG et al. 1990). According to fossil data, the *Ctenomys* radiation is thought to have occurred 1.8 MY ago (ORTELLS 1990; REIG et al. 1990). These evidences strongly suggest that the main mode of speciation has been (and is) chromosomal. The subterranean mode of life plus the populational characteristics of most of the species (small deme size, low vagility) support the chromosomal speciation hypothesis (BIDAU et al. 1996; KING 1993).

In this study we investigate karyotypes of *Ctenomys* from northern Córdoba province (Argentina). The analyzed populations belong to two new biological species, *C. rosendopascuali* and *C. osvaldoreigi* (CONTRERAS 1995 a, b). Our results are compared to previous ones and discussed within the frame of a model for the evolution of the genus which incorporates molecular, morphological, and paleobiogeographical data.

Material and methods

This work is based on the individuals of *Ctenomys* indicated in table 1 and figure 1. All specimens were deposited in the collection of the PROBBAS (CONICET, Corrientes, Argentina), with the following catalogue numbers (sex in parentheses): *C. rosendopascuali.* Mar Chiquita: C-03363 (F), C-03364 (M). Candelaria: C-03464 (M), C-03465 (F). Los Mistoles: C-03509 (M), C-03510 (F). *C. osvaldoreigi.* Estancia San Luis (Sierras Grandes): C-03462 (F), C-03463 (F), C-03977 (F), C-03978 (F), C-03979 (F), C-03980 (F). *C. bergi.* Cruz del Eje: C-03460 (M), C-03461 (M). Las Toscas: C-03506 (M). Salinas Grandes: C-03507 (F). Guanaco Muerto: C-03508 (F).

Mitotic metaphases were obtained following two protocols: direct bone-marrow preparations according to a modified version of FORD and HAMERTON's (1956) technique, and short-term bone-marrow in vitro culture (GIMENEZ and BIDAU 1994). In the first case, bone marrow was incubated in 0.1 ml 0.05 % colchicine plus 9.9 ml 0.075 M KCl for 55 min at 37 °C and subsequently fixed in 3 : 1 methanol : glacial acetic acid. For short-term culture, the tissue was incubated in RPMI 1640 medium supplemented with 15 % foetal calf serum for 20.5 h at 37 °C. A drop of 0.005 % colchicine was then added to the culture, and 15 min later the cells were hypotonized in 0.075 M KCl and fixed in 3 : 1. Nondifferential chromosome staining was performed in phosphate buffered Giemsa (pH = 6.8). G- and C-banding followed the protocols of SEABRIGHT (1971) and SUMNER (1972), respectively. NORs were stained according to HOWELL and BLACK (1980). Meiotic preparations for the observation of sperm morphology were made by the technique of EVANS et al. (1964).

Table 1. Localities, number and sex of the *Ctenomys rosendopascuali*, *C. osvaldoreigi* and *C. bergi* individuals studied.

Locality		N° of specimens	
		Male	Female
	C. rosendopascuali Contreras, 1995		
Mar Chiquita[1]	(30°55′ S–62°41′ W)	1	1
Candelaria	(29°49′ S–63°21′ W)	1	1
Los Mistoles	(30°38′ S–63°54′ W)	1	1
	C. osvaldoreigi Contreras, 1995		
Estancia San Luis[1] (Sierras Grandes)	(31°24′ S–64°48′ W)	–	6
	C. bergi Thomas, 1902		
Cruz del Eje[1]	(30°44′ S–64°48′ W)	1	1
Guanaco Muerto	(30°27′ S–65°01′ W)	–	1
Salinas Grandes	(30°03′ S–65°05′ W)	–	1
Las Toscas	(30°08′ S–64°53′ W)	1	–

[1] Type localities

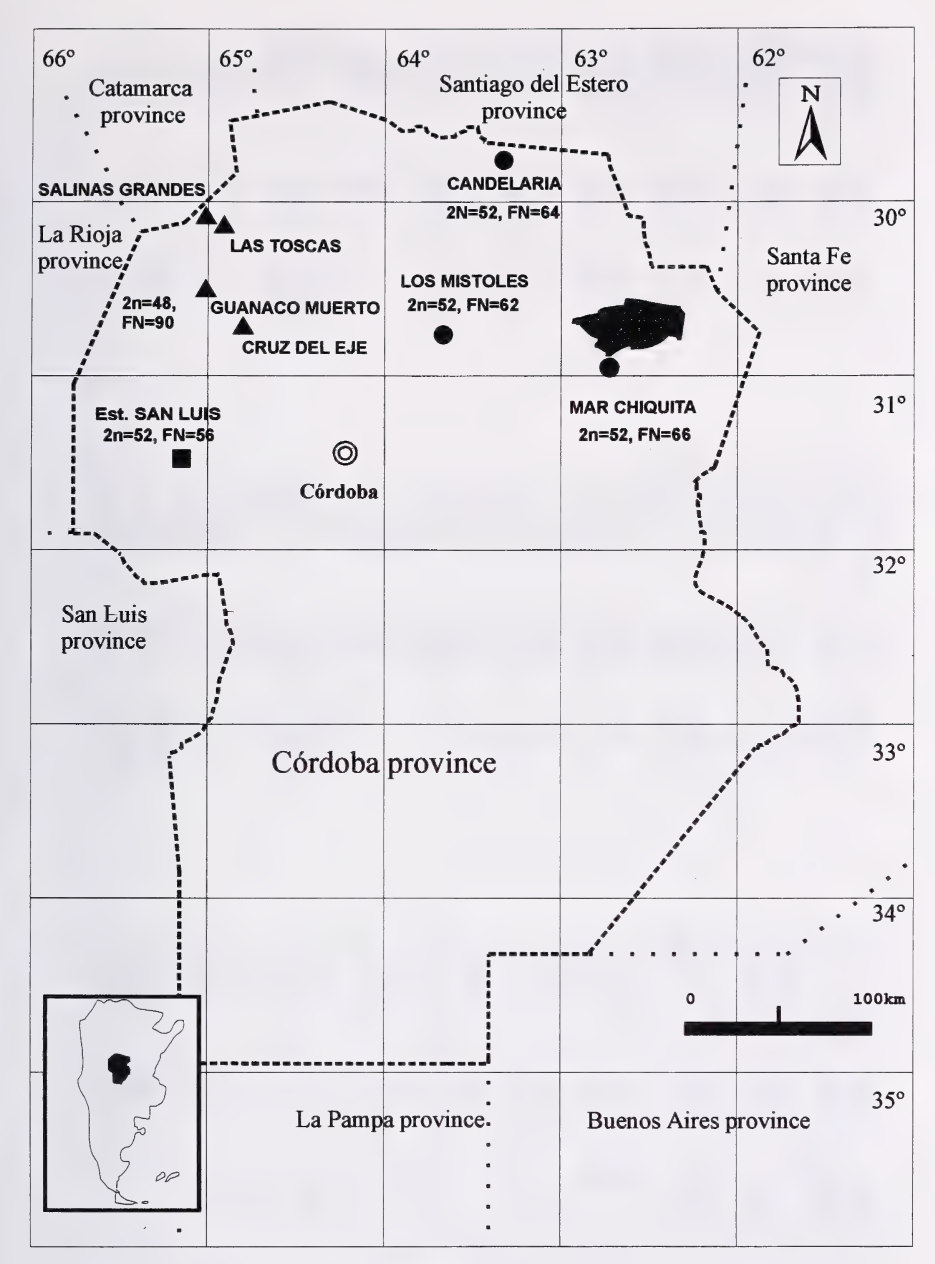


Fig. 1. Geographic distribution of the populations of *Ctenomys rosendopascuali*, *C. osvaldoreigi*, and *C. bergi* analyzed.

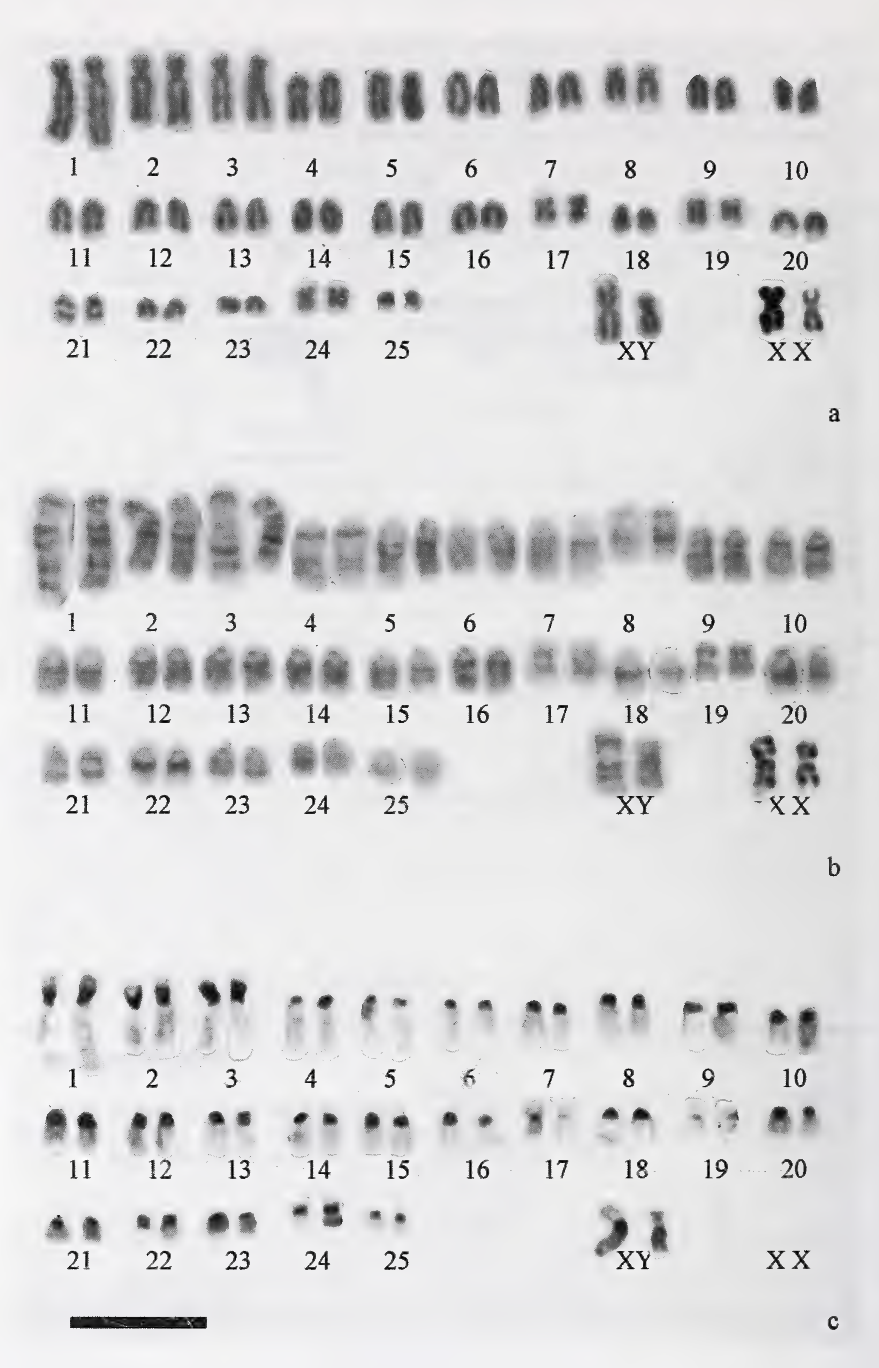


Fig. 2. Karyotype of *C. rosendopascuali* from Mar Chiquita; a. Giemsa stained, b. G-banding, c. C-banding. Bar = 10 µm.

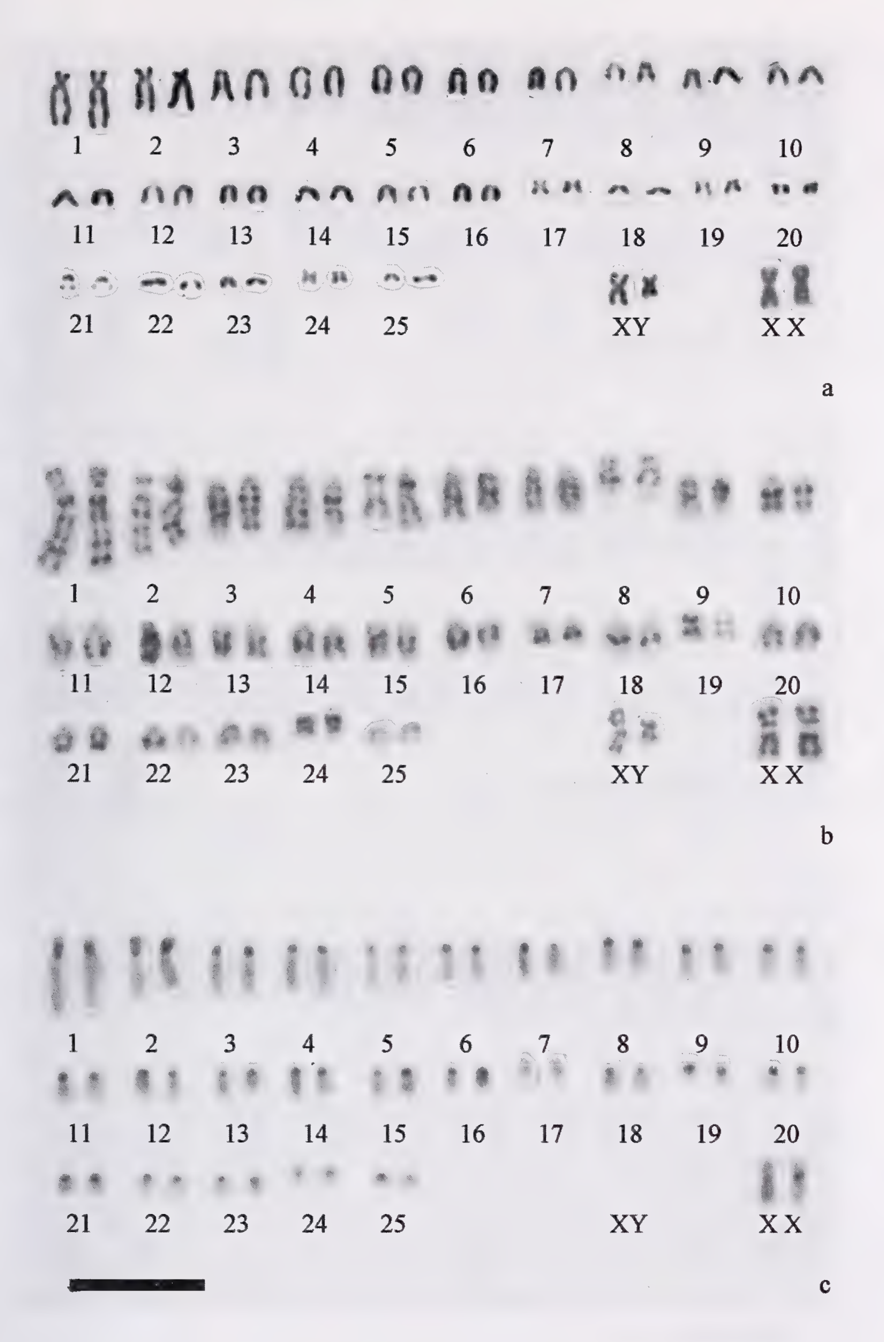


Fig. 3. Karyotype of *C. rosendopascuali* from Candelaria; a. Giemsa stained, b. G-banding, c. C-banding. Bar = 10 µm.

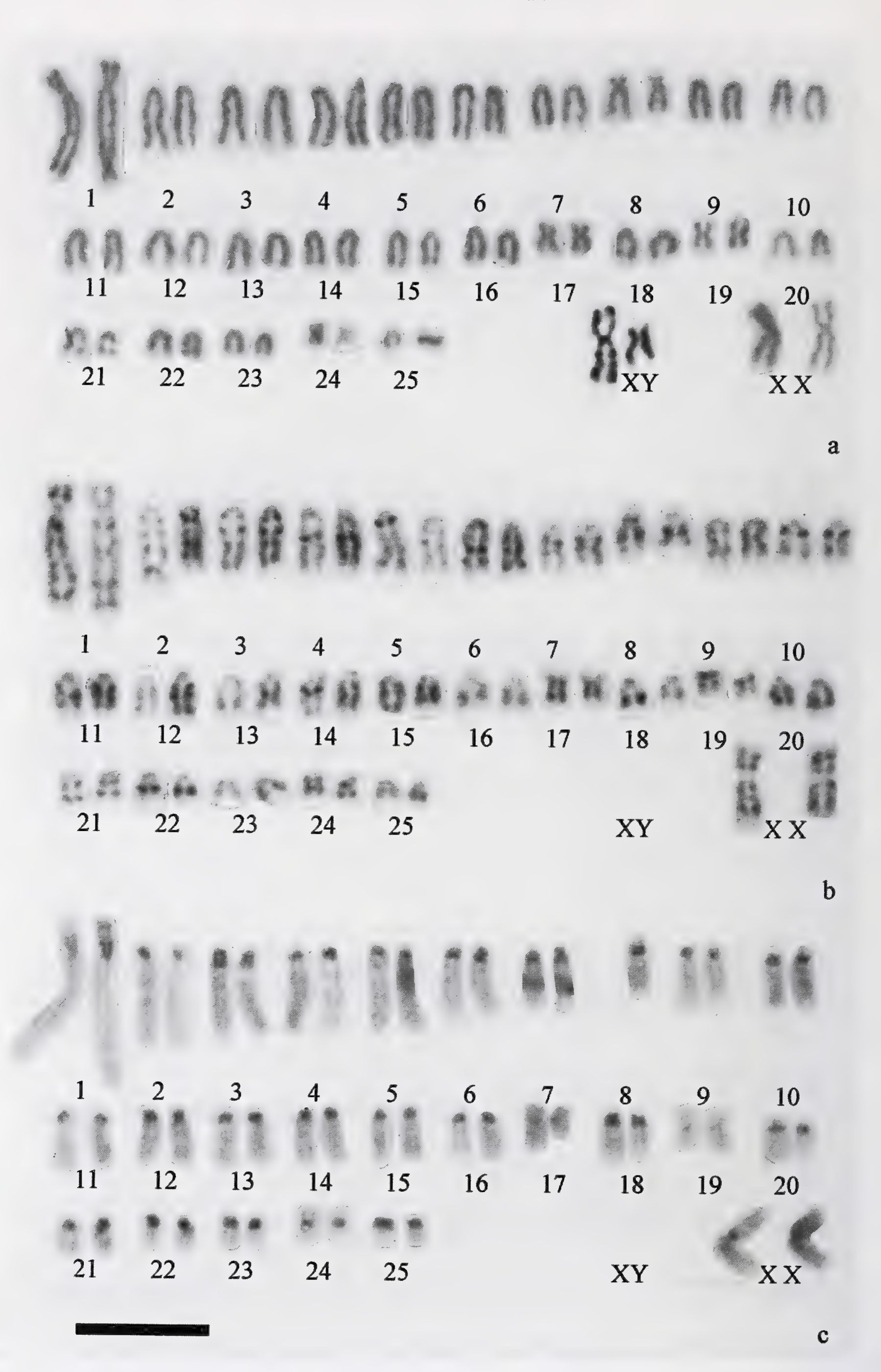


Fig. 4. Karyotype of *C. rosendopascuali* from Los Mistoles; a. Giemsa stained, b. G-banding, c. C-banding. Bar = 10 μm. (Because of technical problems during the production process the second No. 8 chromosome in the third line from bottom is missing!)

Results

C. rosendopascuali

The karyotype of the specimens from Mar Chiquita (the type locality) consists of 2n = 52 chromosomes: pairs 1 to 3 are large subtelocentric autosomes; pairs 4–7, 9–16, 18, 20–23, and 25 are telocentric; the marker pair number 8 is subtelocentric. Pair 21 has an interstitial secondary constriction that represents the single NOR. Pairs 17, 19, and 24 are three small biarmed elements (Figs. 2, 3, 4). The X chromosome is metacentric and represents 7 % of the haploid genome; the Y chromosome is metacentric and small (Fig. 2). FN is thus 66.

Heterochromatin distribution is para- or pericentromeric with prominent C-bands. Pairs 1 to 3 show partially C-positive short arms (Fig. 2 c). Silver impregnation demonstrated that the secondary constriction of pair 19 corresponds to an active interstitial NOR (Fig. 6 a).

The chromosome complement of the animals from Candelaria is basically similar; they are 2n = 52 but instead of 3 pairs of large subtelocentric autosomes only two occur, thus, the FN is reduced to 64 (Fig. 3). A further reduction of the FN to 62 chromosome arms occurs in the 2n = 52 individuals from Los Mistoles which otherwise have a similar karyotype to Mar Chiquita and Candelaria (Fig. 4). Table 2 shows a comparison of relative lengths and centromeric indexes of the three karyotypes.

In the three samples, the distribution of heterochromatin in the autosomes and sex-chromosomes was basically similar. The X-chromosome had a centromeric band while the Y-chromosome showed a uniform intermediate staining. The large biarmed autosomes showed positive C-banding in the pericentromeric region which extended partially to the short arms while the remainder of the autosomes exhibited prominent C-bands in the para- or pericentromeric regions (Figs. 2 c, 3 c, 4 c). Sperm is of the simple asymmetric type.

Table 2. Relative length (RL) and centromeric index (CI) of the chromosomes of four analysed populations of *Ctenomys* from Córdoba. In parentheses, chromosome morphology according to the nomenclature of LEVAN et al. (1964)

	C. rosendopascuali						*C. osvaldoreigi*	
	Mar Chiquita		Candelaria		Los Mistoles		Ea. San Luis	
CN°	RL	CI	RL	CI	RL	CI	RL	CI
1	9.05 ±0.42	22.56 ±0.69 (st)	9.94 ±0.22	20.87 ±1.38 (st)	10.56 ±0.54	21.87 ±0.68 (st)	11.23 ±0.20	0 (t)
2	6.77 ±0.31	28.36 ±0.64 (sm)	7.67 ±0.29	20.68 ±1.46 (st)	6.55 ±0.22	0 (t)	6.99 ±0.09	0 (t)
3	6.75 ±0.32	24.24 ±0.98 (st)	5.82 ±0.11	0 (t)	5.85 ±0.09	0 (t)	6.49 ±0.08	0 (t)
4	5.33 ±0.10	0 (t)	5.67 ±0.04	0 (t)	5.70 ±0.10	0 (t)	6.16 ±0.13	0 (t)
5	5.10 ±0.10	0 (t)	5.27 ±0.12	0 (t)	5.38 ±0.15	0 (t)	5.29 ±0.23	0 (t)
6	4.28 ±0.13	0 (t)	4.59 ±0.11	0 (t)	4.80 ±0.09	0 (t)	4.68 ±0.08	0 (t)
7	4.25 ±0.10	0 (t)	4.29 ±0.08	0 (t)	4.10 ±0.13	0 (t)	4.39 ±0.05	0 (t)
8	4.30 ±0.29	18.73 ±0.98 (st)	4.07 ±0.06	19.97 ±1.05 (st)	3.70 ±0.07	15.28 ±0.33 (st)	4.06 ±0.13	16.65 ±1.16 (st)

Table 2. Continued.

	C. rosendopascuali						*C. osvaldoreigi*	
	Mar Chiquita		Candelaria		Los Mistoles		Ea. San Luis	
CN°	RL	CI	RL	CI	RL	CI	RL	CI
9	3.95 ±0.14	0 (t)	3.92 ±0.06	0 (t)	3.63 ±0.07	0 (t)	4.04 ±0.09	0 (t)
10	3.68 ±0.10	0 (t)	3.66 ±0.05	0 (t)	3.57 ±0.07	0 (t)	3.82 ±0.09	0 (t)
11	3.47 ±0.09	0 (t)	3.47 ±0.08	0 (t)	3.52 ±0.08	0 (t)	3.69 ±0.06	0 (t)
12	3.26 ±0.14	0 (t)	3.43 ±0.07	0 (t)	3.40 ±0.06	0 (t)	3.52 ±0.05	0 (t)
13	3.26 ±0.15	0 (t)	3.28 ±0.08	0 (t)	3.31 ±0.05	0 (t)	3.19 ±0.10	0 (t)
14	3.14 ±0.10	0 (t)	3.24 ±0.09	0 (t)	3.28 ±0.04	0 (t)	3.04 ±0.11	0 (t)
15	3.13 ±0.10	0 (t)	3.11 ±0.08	0 (t)	3.12 ±0.06	0 (t)	2.94 ±0.08	0 (t)
16	2.87 ±0.10	0 (t)	2.95 ±0.07	0 (t)	2.99 ±0.07	0 (t)	2.85 ±0.23	41.85 ±1.08 (m)
17	2.87 ±0.06	41.67 ±2.41 (m)	2.49 ±0.12	45.72 ±1.53 (m)	2.51 ±0.14	40.71 ±0.56 (m)	2.74 ±0.05	0 (t)
18	2.79 ±0.13	0 (t)	2.67 ±0.11	0 (t)	2.80 ±0.13	0 (t)	2.44 ±0.10	45.00 ±1.87 (m)
19	2.56 ±0.06	43.24 ±2.04 (m)	2.29 ±0.15	47.12 ±0.64 (m)	2.41 ±0.11	43.92 ±1.56 (m)	2.31 ±0.10	0 (t)
20	2.52 ±0.13	0 (t)	2.36 ±0.14	0 (t)	2.55 ±0.04	0 (t)	2.17 ±0.09	0 (t)
21	2.35 ±0.12	0 (t)	2.36 ±0.10	0 (t)	2.45 ±0.09	0 (t)	2.06 ±0.06	0 (t)
22	2.30 ±0.11	0 (t)	2.06 ±0.07	0 (t)	2.20 ±0.09	0 (t)	1.76 ±0.04	0 (t)
23	2.18 ±0.12	0 (t)	1.93 ±0.07	0 (t)	1.97 ±0.02	0 (t)	1.69 ±0.05	0 (t)
24	2.14 ±0.06	47.96 ±0.24 (m)	2.27 ±0.13	47.48 ±0.27 (m)	1.96 ±0.09	44.28 ±1.63 (m)	1.60 ±0.08	0 (t)
25	2.00 ±0.07	0 (t)	1.50 ±0.05	0 (t)	1.55 ±0.03	0 (t)	1.36 ±0.04	0 (t)
X	5.96 ±0.49	41.39 ±1.32 (m)	5.67 ±0.19	39.52 ±1.09 (m)	6.16 ±0.26	39.09 ±0.85 (m)	5.56 ±0.14	36.66 ±1.85 (sm)
Y	4.11 ±0.14	29.62 ±2.25 (sm)	3.48 ±0.26	32.52 ±0.57 (sm)	3.73 ±0.15	32.43 ±0.67 (sm)	*	*

Notes: CN° = chromosome number. Relative length (RL) was calculated as the length percentage of each chromosome pair per haploid complement. Centromeric Index (CI) was calculated according to Levan et al. (1964) as Length of Short Arm × 100/Total Chromosome Length. Thus chromosomes are classified as m if CI = 50–37.5, sm if CI = 37.5–25.0, st if CI = 25.0–12.5 and t if CI = 12.5–0. In all cases, Standard Error is indicated. * No information is available on the Y chromosome of *C. osvaldoreigi*.

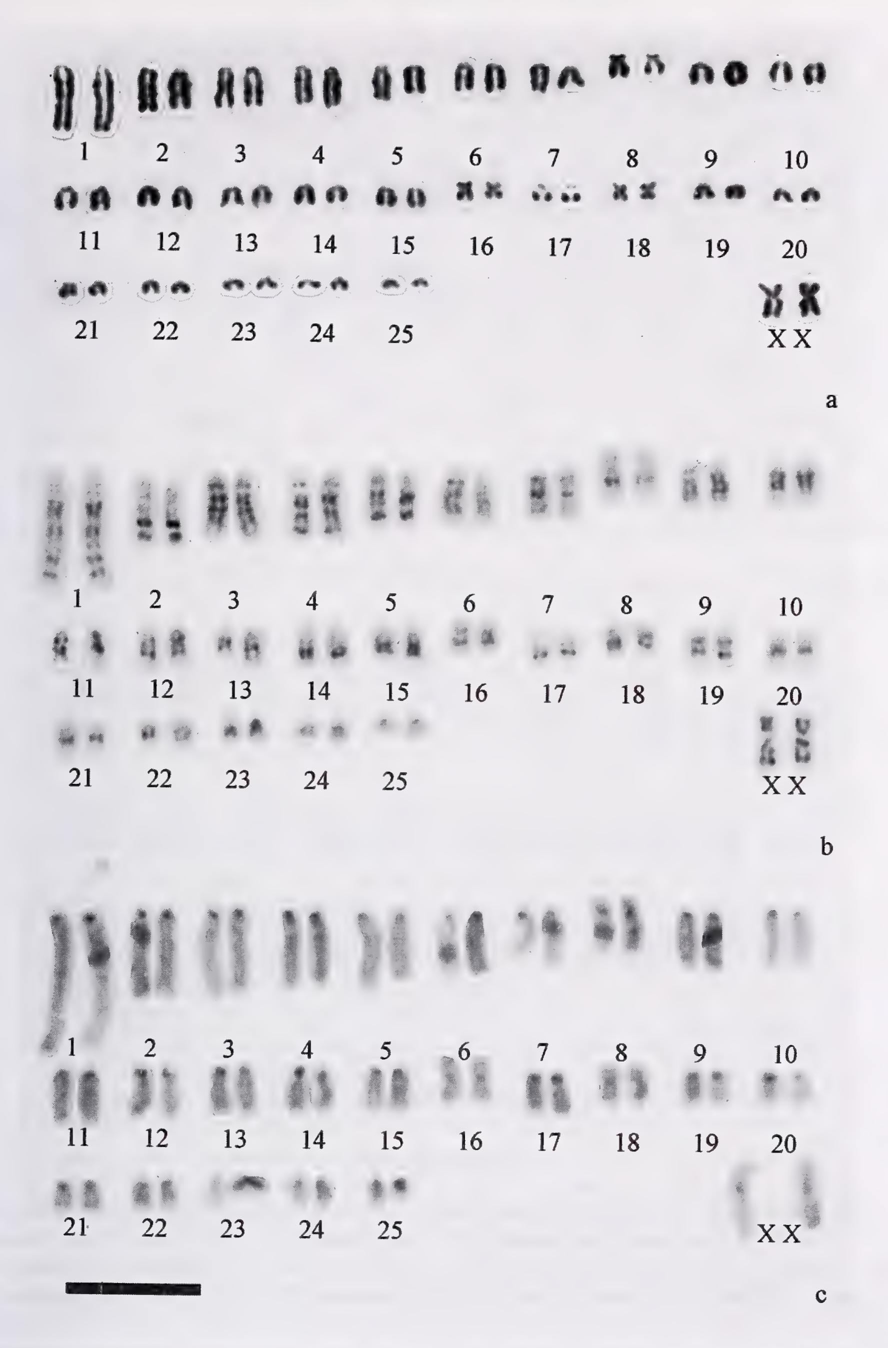


Fig. 5. Karyotype of *C. osvaldoreigi* from Estancia San Luis; a. Giemsa stained, b. G-banding, c. C-banding. Bar = 10 μm.

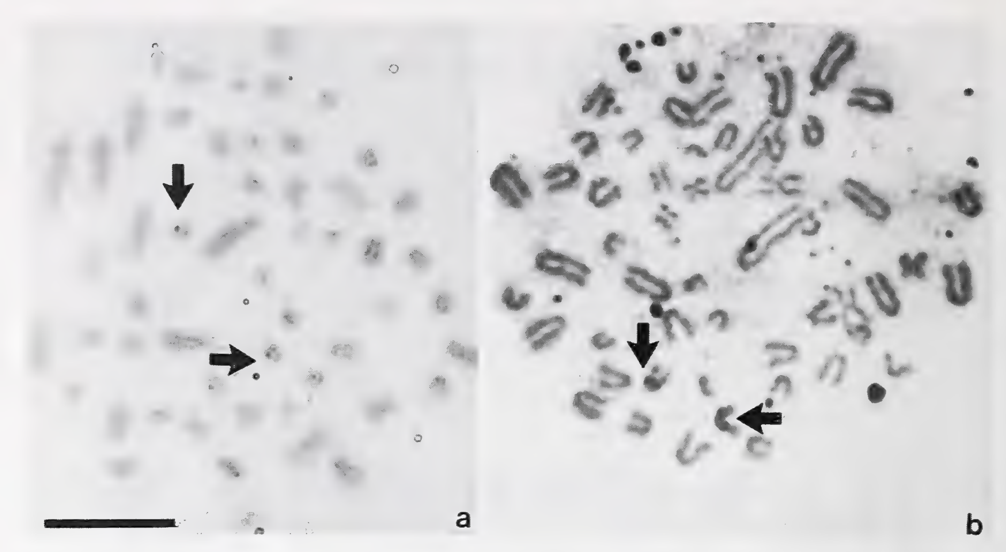


Fig. 6. Silver staining of NORs in (a) *C. rosendopascuali* from Mar Chiquita and (b) *C. osvaldoreigi*. Arrows indicate the NOR carrying autosomes. Bar = 10 μm.

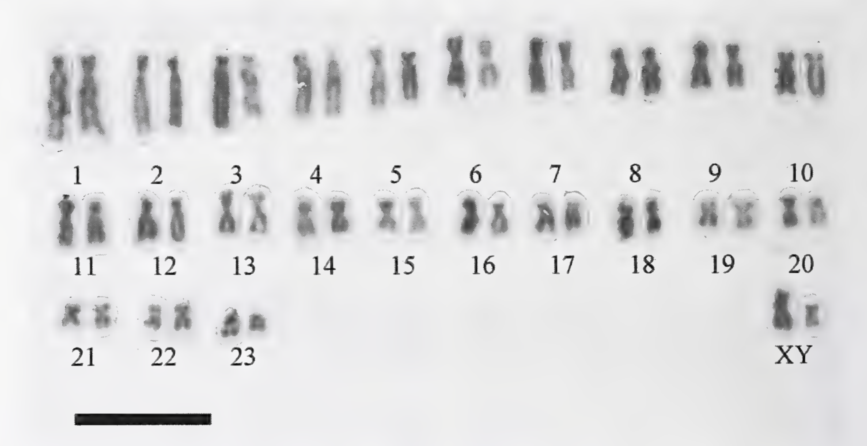


Fig. 7. Giemsa stained karyotype of *Ctenomys bergi* from Cruz del Eje. Bar = 10 μm.

C. osvaldoreigi

The specimens from the Sierras Grandes were collected at more than 2 000 m above sea level at Estancia San Luis (the type locality). The karyotype of these individuals is very similar to the previously described forms (Fig. 5) and consists of seven pairs of telocentric autosomes of decreasing size, the marker subtelocentric pair n °8, telocentric pairs 9 to 15, 17, and 19–25 which decrease gradually in size and two small metacentric pairs: 16 and 18 (Tab. 2). Pair 17 carries the single NOR but in this case, the secondary constriction is procentric (Fig. 6 b) which differentiates it from the other specimens in which the NOR is interstitial. The X chromosome is a large metacentric. Since no males were karyotyped, no information on the Y chromosome is available. C-banding revealed that the chromosomes have a small amount of centric constitutive heterochromatin (Fig. 5 c). Sperm is of the simple asymmetric type.

C. bergi

In order to compare the karyotypes of the new species with other forms of the general geographic area, we examined samples from four populations of *C. bergi* from northwestern Córdoba province, including the type locality. The karyotype of this species had already been described by Reig et al. (1990) from a single locality. Our results confirmed the published karyotype of 2n = 48 and FN = 90 which consists of 22 pairs of biarmed autosomes of different morphologies and a single telocentric pair which carries the NOR; both the X and the Y chromosomes are metacentric (Fig. 7). A number of short arm heteromorphisms was detected, probably due to the heterochromatic nature of these arms, but they will be described elsewhere. This species has a symmetric sperm.

Discussion

Ctenomys includes more than 60 species distributed through an extensive area of South America. The amount of knowledge already accumulated including morphological, biogeographical, paleontological, chromosomal, genetic, and molecular data (Bidau et al. 1996; Contreras, 1996; Giménez et al. 1996; Mirol et al. 1995 a, b; Ortells, 1990, 1995; Reig et al. 1990) allows the formulation of preliminary interpretations of its evolutionary history that dates back to the Pliocene (Contreras et al. 1997). An ancestral stock which evolved in and expanded from the northern highlands of Bolivia and Perú is considered. *C. opimus* would be the closer extant form to the ancestral stock. From the latter, a number of species that occupy the area of the ancestral stock, evolved. These forms retain a certain degree of plesiomorphism and include: *C. frater*, *C. tuconax*, *C. scagliai*, *C. knighti* (all with symmetric sperm) and *C. osvaldoreigi* (with simple asymmetric sperm). The same primitive stock gave rise along its southward expansion and differentiation to the so-called "chacoan" and "parachacoan" species. The first of these branches consists of *C. boliviensis*, *C. goodfellowi*, *C. nattereri*, and *C. rondoni* (with symmetric sperm). A closely related species sequence includes *C.* sp. (from Chuquisaca, Bolivia), *C. conoveri* and *C.* sp. (from Eastern Paraguay), all of them with a tendency towards gigantism and symmetric sperm. Further south, another sequence includes *C. scagliai*, *C. tucumanus*, *C. occultus*, *C. latro*, *C. argentinus*, and *C. pilarensis*, also with symmetric sperm. In "parachacoan" areas and originating from *C. osvaldoreigi* from the Sierras Grandes (Córdoba province, Argentina) derives the *C. rosendopascuali* sequence of the northern plains of Córdoba, and *C. yolandae* from Santa Fe which in turn is related with a complex of mesopotamic and Uruguayan species and with *C. bonettoi* that expands northwards towards the Chaco (Giménez et al. 1996, 1997). All the latter forms have simple asymmetric sperm.

There is a close chromosomal relationship between *C. osvaldoreigi* and *C. rosendopascuali* which is in agreement with their morphological affinities (Contreras 1995 a, b). In fact, only three fixed karyotypic differences occur between both species: 1) The position of the secondary constriction in the chromosome pair carrying the NOR, which is proximal in *C. osvaldoreigi* and interstitial in *C. rosendopascuali* and perhaps due to a paracentric inversion; 2) The existence of a third small metacentric autosomal pair in *C. rosendopascuali*; and 3) The biarmed nature of chromosome n° 1 in the three analyzed populations of the latter species. The other two chromosomal differences are polytypic and probably of more recent origin. Chromosomal polytypism and polymorphism are not infrequent in *Ctenomys* and have been reported in very different species involving many kinds of chromosomal rearrangements (Bidau et al. 1996; Giménez et al. 1996, 1997; Ortells 1995; Ortells et al. 1990; Freitas 1994). This chromosomal variation is a small-scale reflection of the general situation of the genus, in which chromosomal speciation has probably been central to its "explosive" radiation (Bidau et al. 1996;

Reig et al. 1990). Thus, chromosomal polytypisms could represent potential incipient stages of chromosomal speciation (Giménez et al. 1997). It must be noted, however, that different classes of chromosomal rearrangements have widely different effects on heterozygote fertility and thus, their involvement in reproductive isolation and speciation must be regarded cautiously (Bidau 1991; Contreras et al. 1990; King 1993; White 1973, 1978).

The origin of the large biarmed chromosomes of *C. rosendopascuali* can be interpreted, on the basis of G- and C-band homologies, as a sequence of rearrangements start-

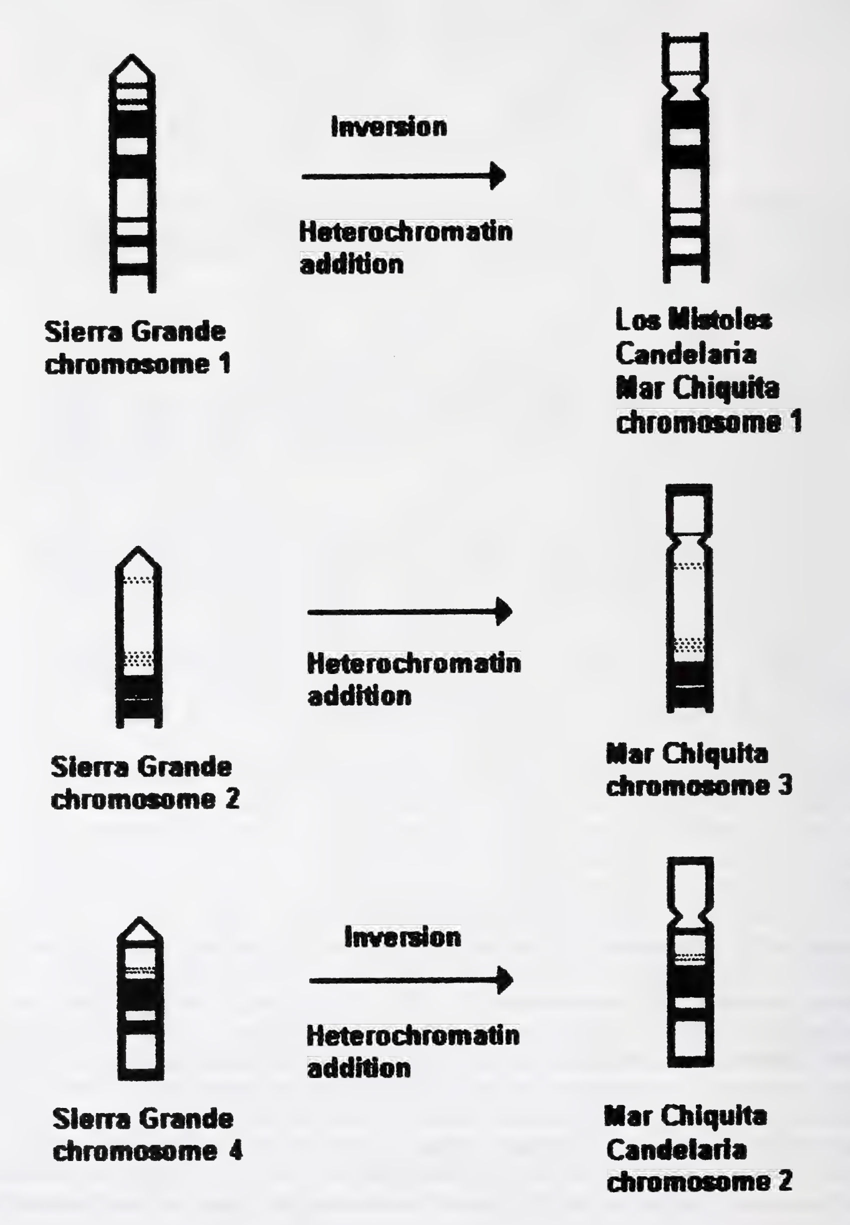


Fig. 8. Main chromosomal relationships between *Ctenomys rosendopascuali* and *C. osvaldoreigi*.

ing with the karyotype of *C. osvaldoreigi* (Fig. 8) which is assumed as ancestral according to the morphological evidence (Contreras 1995 a, b; Contreras et al. 1990). Pair n° 1 of this species, which is present throughout its whole range, originated through a pericentric inversion and increase in heterochromatin content. Pair n° 2, present in the Mar Chiquita and Candelaria populations, also arose by a pericentric inversion and heterochromatin addition from the standard chromosome n° 4 of *C. osvaldoreigi*. Pair n° 3 of the Mar Chiquita individuals is restricted to this population and is probably of recent origin; it arose by heterochromatin addition that produced the short arm, from pair n° 2 of *C. osvaldoreigi*. Karyotypic evolution through heterochromatin variation seems to be a common mechanism in *Ctenomys* (Freitas 1994; Massarini et al. 1991) although its meaning is still obscure.

The study of *C. osvaldoreigi* and *C. rosendopascuali* poses a number of questions regarding the general relationships of the *Ctenomys* species. First, it led us to question the validity of karyotypic comparisons for the detection of evolutionary relationships within the genus. It is true that both species were originally identified by the unique character of their karyotypes which led to a detailed taxonomic study and their description as new species (Contreras 1995 a, b). However, the chromosomal relationship of the more plesiomorphic form, *C. osvaldoreigi*, with the species to which it is taxonomically closer, is obscure. For example, *C. tuconax* is 2 n = 58–61, FN = 80; *C. scagliai* is 2 n = 36, FN = 64; *C. opimus* is 2 n = 26, FN = 48 (Ortells 1990) and *C. frater*, 2 n = 52, FN = 78 (Cook et al. 1990). Although detailed comparisons of banded karyotypes (which are in progress) are needed, this small sample of chromosomal variation is a clear indication of the difficulties involved in this type of analysis. Furthermore, the lack of knowledge about the ancestral karyotype of the genus makes the establishment of directions of chromosome change impossible at present. It is true that diploid numbers of 2 n = 48 and 2 n = 50 are common within different lineages within the genus; however, these numbers are almost always associated with high FN's as clearly demonstrated by the *C. bergi* specimens studied here, which show the largest FN (90) yet found within the genus. Thus, the presence of a 2 n = 52 with relatively low FN in a primitive form such as *C. osvaldoreigi* is relevant because of its rarity, and it is interesting that *C. opimus* (the extant form which is considered to be closely related to the ancestral *Ctenomys* stock; Contreras et al. 1990) is 2 n = 26 and FN = 48 (all the autosomes being biarmed); thus, a Robertsonian (fusion/fission) relationship could exist between both species which of course, will have to be proved through banded karyotype comparisons. The complex nature of the interpretation of cytogenetic data in this genus is further demonstrated by the fact that the species which shows the closest karyotypic affinities with *C. osvaldoreigi* and *C. rosendopascuali* is *C. pilarensis* from Paraguay which as noted above, belongs to a different progeny (Giménez et al. 1996); its polytypic karyotype is also characterized by 2 n = 48–50 and a low FN (50). This similarity could reflect a common primitive condition for both independent lineages.

Two further problems deserve discussion. First, both species have the simple asymmetrical type of sperm while they belong according to other evidence to a group of forms that have the purportedly primitive character state, i. e., the symmetrical sperm (Contreras 1996; Vitullo et al. 1988; Vitullo and Cook 1991). It is thus tempting to assign *C. osvaldoreigi* or an immediate ancestor, the role of having generated the novel asymmetric sperm. This could explain why the putatively derived species *C. yolandae* and *C. bonettoi* have asymmetrical sperm (complex asymmetrical in the case of the first species); however, the Chilean species of *Ctenomys* also have asymmetrical sperm and their affinities to Argentinian species is obscure. It is at least possible that the asymmetrical sperm condition evolved independently in more than one lineage.

Finally, *C. rosendopascuali* and *C. osvaldoreigi* were studied as part of a project to construct a molecular phylogeny of the genus using analysis of cytochrome b sequences of

mtDNA (Mirol et al. 1995 a, b). Our preliminary results confirm the ancestral nature of *C. osvaldoreigi* but indicate a rather distant relationship with *C. rosendopascuali* which is very close to *C. yolandae* and surprisingly, to *C. bergi*. These results further stress a paradox that is not unique to *Ctenomys*: taxa that speciate rapidly via chromosomal means are probably less readily explainable in evolutionary terms based solely on chromosomal arrangement.

Acknowledgements

This work was partially financed through a British Council-Fundación Antorchas grant to C. J. B. The authors affiliated to the CONICET gratefully acknowledge its continuous support. M. D. G., C. J. B., and C. F. A. were benefited by the Sistema Nacional de Incentivos a la Investigación of the Secretaría de Ciencia y Técnica (Argentina).

Zusammenfassung

Chromosomale Charakterisierung und karyologische Beziehungen zwischen zwei neuen Arten von Ctenomys (Rodentia, Ctenomyidae) aus dem Norden der Provinz Córdoba, Argentinien

Die Karyotypen zweier neu beschriebener *Ctenomys*-Arten aus dem nördlichen Teil der Provinz Córdoba wurden untersucht. *C. osvaldoreigi* ist nur aus der Terra typica der Art in den über 2 000 m Seehöhe gelegenen Tälern der Sierras Grandes bekannt. Der Karyotyp bestand aus 2 n = 52 Chromosomen mit FN = 56 und umfaßte 22 Paar graduell in der Größe abnehmender telozentrischer Autosomen, ein Paar subtelozentrischer Autosomen (Nr. 8), zwei Paar kleiner metazentrischer Chromosomen sowie ein Paar Geschlechtschromosomen. Bei *C. rosendopascuali* wurden drei Populationen aus den nordöstlichen Ebenen der Provinz Córdoba analysiert, wobei eine der Populationen in der Terra typica der Art lag. Alle Individuen hatten 2 n = 52, aber die FNs der drei Populationen unterschieden sich voneinander. Die Tiere aus Los Mistoles zeigten FN = 62; der Karyotyp bestand aus einem Paar großer subtelozentrischer Autosomen, einem mittelgroßen subtelozentrischen Chromosomenpaar (Nr. 8), zwanzig telozentrischen Paaren, drei kleinen metazentrischen Paaren sowie einem Paar Geschlechtschromosomen. Bei den Tieren aus Candelaria war FN = 64; der Karyotyp zeigte ein zweites großes subtelozentrisches Chromosomenpaar als Ersatz für ein großes telozentrisches Paar, während der restliche Chromosomenbestand jenem in Los Mistoles ähnlich war. Ein weiteres großes subtelozentrisches Paar kam in der Mar Chiquita-Population vor. FN war daher 66; der restliche Karyotyp unterschied sich jedoch nicht von den Karyotypen der beiden anderen Populationen. Um die neuen Arten einer bekannten Art aus demselben geographischen Raum gegenüberzustellen, wurden vier Populationen von *C. bergi* aus dem nordwestlichen Córdoba karyotypisiert. Alle Individuen zeigten 2 n = 48, FN = 90. Die drei bei *C. rosendopascuali* gefundenen Karyotypen sind einander auffällig ähnlich und über relativ einfache Umgruppierungen auch jenem von *C. osvaldoreigi* verwandt, was die morphologische und molekulare Nähe der beiden Arten unterstreicht.

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Z. Säugetierkunde **64** (1999) 107–109
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Zwei neue Nachweise der Weißrandfledermaus (*Pipistrellus kuhli*) für Deutschland

Von W. Fiedler, H. U. Alder und Pia Wohland

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Eingang des Ms. 06. 10. 1998
Annahme des Ms. 21. 10. 1998

Key words: Kuhl's pipistrelle, Southern Germany, Lake of Constance, range expansion

Am 3. 7. 1998 wurde im Stadtgebiet von Konstanz (westlicher Bodensee-Raum, Baden-Württemberg, Deutschland) ein unselbständiges und nicht flugfähiges, etwa 14 Tage altes Jungtier der Weißrandfledermaus (*Pipistrellus kuhli*) von Passanten auf der Straße aufgegriffen und uns übergeben. Wenige Wochen später, am 9. 9. 1998 wurde nur etwa 3 km entfernt ein adultes Männchen der selben Art gefunden, das auf dem Balkon eines Wohnhauses in eine Gießkanne gefallen war. Beide Tiere konnten nach Pflege wieder in die Freiheit entlassen werden und stellen zusammen mit einem Fund 1995 nördlich von Basel (Gebhard 1997) die ersten dokumentierten Nachweise der Weißrandfledermaus in Deutschland dar.

Zur Artbestimmung haben wir in erster Linie das charakteristische Erscheinungsbild der vorderen Zähne im Oberkiefer herangezogen: Incisivus^1 ist bei der Weißrandfledermaus gegenüber allen anderen europäischen Vertretern der Gattung *Pipistrellus* einspitzig, Incisivus^2 und Praemolar^1 sind beide sehr klein, letzterer von außen in der Zahnreihe überhaupt nicht sichtbar (z. B. Schober und Grimmberger 1987). Weitere, an den beiden Findlingen festgestellte Unterschiede zu den im selben Gebiet regelmäßig auftretenden Zwerg- und Rauhhautfledermäusen (*Pipistrellus pipistrellus, P. nathusii*) waren eine geringfügig hellere Färbung des Rückenfells, dazu kontrastierende, dunklere und etwas schmalere Ohren sowie eine sehr deutliche, schmutzigweiße Außenkante im körpernahen Bereich der Armflughaut. Der Protestruf des Jungtiers war nicht zischend-kreischend wie bei jungen Zwergfledermäusen, sondern war – an die Kontaktrufe junger Mausohren (*Myotis myotis*) erinnernd – aus rasch aufeinanderfolgenden, klar trennbaren, hohen Einzellauten zusammengesetzt. Vom ersten Fund existieren Belegfotos, ferner waren wir durch Arbeiten in der Schweiz und Italien mit der Artbestimmung bei Weißrandfledermäusen nicht unerfahren.

Das Verbreitungsgebiet der Weißrandfledermaus reicht von Spanien ostwärts bis Pakistan, umfaßt den gesamten Mittelmeerraum und erstreckt sich über den afrikanischen Kontinent mit Ausnahme der trockensten Bereiche der Sahara und Südwestafrikas bis zur Republik Südafrika. Die nordöstliche Verbreitungsgrenze verläuft derzeit etwa entlang einer Linie Seine–Hochrhein–Drau durch West- und Mitteleuropa (Benjamini 1987; Richarz und Limbrunner 1992; Stutz und Haffner 1995; Kingdon 1997 sowie die weiter unten genannten Funde). Im Mittelmeer-Raum gilt die Art als häufig (Stutz und

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Haffner 1995; Benjamini 1987). Eine offenkundige Nordostverschiebung der Arealgrenze seit den 1980er Jahren wird durch eine Reihe von Funden dokumentiert. Gebhard (1983) vermutet für die beiden von ihm genannten Funde in Basel (Nordwestschweiz) von 1935 und 1979 noch eine mögliche Verfrachtung der Tiere per Eisenbahn aus südlichen Landesteilen. Bereits fünf Jahre später meldet er anhand weiterer Funde deutliche Hinweise auf eine Etablierung der Art in der Region Basel (Gebhard 1988) und 1995 gelang ihm in Weil am Rhein unmittelbar an der schweizer Grenze der erste Fund auf deutschem Gebiet (Gebhard 1997). Im Verlauf der 1980er und frühen 1990er Jahre gelangen nach Stutz und Haffner (1992) 11 Funde, darunter 6 Wochenstubennachweise, auf der Alpennordseite der Ostschweiz. Seit 1995 wird die Art regelmäßig im schweizerischen Schaffhausen (ca. 40 km westlich des hier genannten Fundortes Konstanz gelegen) angetroffen, wo 1996 der erste Fortpflanzungsnachweis gelang (Nachweis durch H. U. Alder). Die erste Wochenstube im schweizer Ort Kreuzlingen, der mit Konstanz ein urbanes Kontinuum bildet, erfolgte 1997 (Burkhard und Burkhard 1997). Auch aus Österreich ist durch Spitzenberger und Walder (1993) mit einem Erstnachweis aus Innsbruck (Tirol) das neue Auftreten von Weißrandfledermäusen nördlich des Alpen-Hauptkammes dokumentiert. Die beiden Konstanzer Nachweise fügen sich in das dargestellte Bild einer rezenten Nordostverschiebung der Arealgrenze gut ein (Abb. 1).

Die enge Bindung an menschliche Siedlungen, die die Weißrandfledermaus auch südlich der Alpen zeigt (Stutz und Haffner 1995), dürfte es der wenig wandernden und wohl überwiegend ortstreuen Art erleichtert haben, in klimatisch milden Siedlungs-Agglomerationen nördlich der Alpen Fuß zu fassen. Ob und inwieweit diese Arealausweitung auf eine derzeit für die zurückliegenden Jahre diskutierte Klimaerwärmung zurückzuführen ist, bedarf genauerer Klärung. Als bemerkenswerte Analogie aus der Vogelwelt sei z. B. auf Alpensegler (*Apus melba*), Bienenfresser (*Merops apiaster*) oder

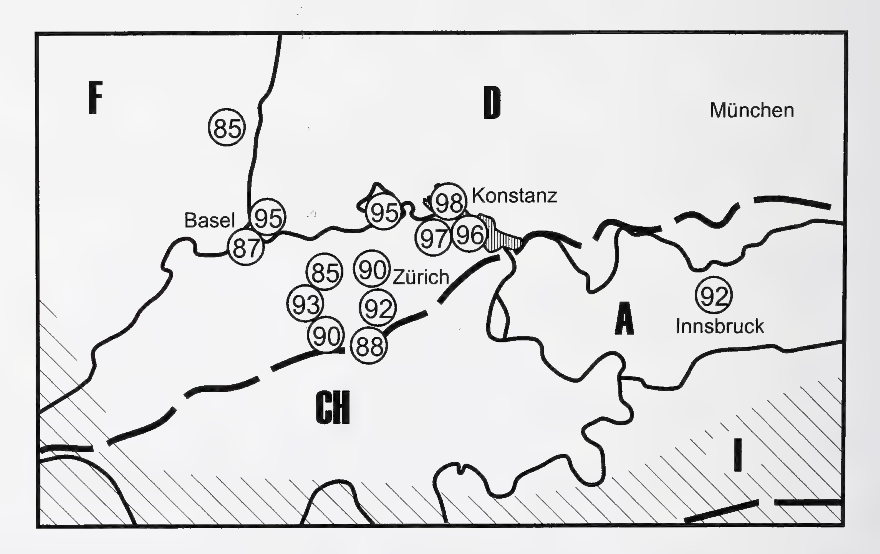


Abb. 1. Nachweise der Weißrandfledermaus *Pipistrellus kuhli* in Mitteleuropa. Schräg schraffiert: regelmäßige Verbreitung bereits vor den 1980er Jahren; Kreise: Nachweise mit Jahreszahl des ersten Fundes; dicke durchbrochene Linie: Nord- und Südkante der Alpen; dünne durchgezogene Linien: Landesgrenzen. 2 frühere Nachweise aus Basel sind wegen möglicher künstlicher Verfrachtung nicht berücksichtigt (siehe Text). Nach Gebhard (1988, 1997); Spitzenberger und Walder (1993), Stutz und Haffner (1995), Burkhard und Burkhard (1997), sowie Daten der Koordinationsstelle Ost für Fledermausschutz, Zürich.

Schwarzkopfmöwe (*Larus melanocephalus*) hingewiesen, die ihre noch zur Mitte dieses Jahrhunderts mediterranen Brutgebiete in neuerer Zeit nach Mittel- und sogar Nordeuropa ausgedehnt haben (Burton 1995).

Für das Aufsuchen von Fledermausquartieren sowie die vorübergehende Aufnahme aufgegriffener Fledermäuse liegt uns eine Ausnahmegenehmigung des Regierungspräsidiums Freiburg (Az. 73/8852.46) vor.

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Anschr. der Verf.: Dr. Wolfgang Fiedler und Pia Wohland, Forschungsstelle für Ornithologie der Max-Planck-Gesellschaft, Vogelwarte Radolfzell, Schloß Möggingen, D-78315 Radolfzell, Deutschland; Hansueli Alder, Regionaler Fledermausschutzexperte des Kanton Schaffhausen, Alpenstr. 79, CH-8200 Schaffhausen, Schweiz

Z. Säugetierkunde **64** (1999) 110–115

http://www.urbanfischer.de/journals/saeugetier

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Comparative measurements of terrestrial and aquatic locomotion in *Mustela lutreola* and *M. putorius*

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Receipt of Ms. 22. 05. 1998
Acceptance of Ms. 16. 11. 1998

Key words: *Mustela lutreola*, *Mustela putorius*, locomotion, swimming

Through the evolutionary history of mammals, the transition to a semi-aquatic way of life led to different morphological adaptations and behavioural adjustments facilitating more particularly the locomotion in water (Lessertisseur and Saban 1967; Alexander 1982; Renous 1994). However, the requirements of locomotory adaptation to an aquatic habitat directly affected terrestrial mobility (Schmidt-Nielsen 1972; Tarasoff et al. 1972; Renous 1994).

Different studies on the American mink *Mustela vison* have stressed that the semi-aquatic way of life of this mustelid resulted from a compromise among these contradictory requirements (Poole and Dunstone 1976; Dunstone 1978; Kuby 1982; Williams 1983 a). Ethological adaptations to the exploitation of water habitats allowed this species to adapt to an ecological niche between the Lutrinae and the more terrestrial weasels (Burt and Gossenheider 1952; Hall et al. 1959; Halley 1975; Williams 1983 a). In the Palearctic, two autochthonous mustelids, the European polecat *Mustela putorius* and the European mink *Mustela lutreola*, were intermittent to respective niches of typical terrestrial mustelids, such as the stoat *Mustela erminea* and more aquatic ones such as the otter *Lutra lutra* (Bourliere 1955; Saint-Girons 1973; Brosset 1974; Grzimek 1974). Although morphologically very similar, *Mustela lutreola* is a characteristic semi-aquatic animal, whereas *Mustela putorius* is to a greater extent considered to be a mainly terrestrial predator (Saint-Girons 1973; Stubbe 1993; Lodé 1997). Both mustelids frequent marshes and forest brooks (Heptner et al. 1974; Danilov and Rusakov 1969; Blandford 1987; Pikuliik and Sidorovich 1991; Brzezinski et al. 1992) but the home-range of the European mink remains rather linear along water courses (Palazon and Ruiz-Olmo 1993), whereas the activity area of the polecat is more strongly determined according to the surface (Weber 1989; Lodé 1993, 1994). One might reasonably suppose that the semi-aquatic way of life would have led to important behavioural modifications when compared to *Mustela putorius*. The aim of this study was to evaluate the locomotory abilities of these two species, mainly the mode of moving on ground and swimming in water.

The study took place in western France, in Sévérac and Chizé Zoorama in summer 1995 and concerned four *Mustela putorius* (two adult females, body weight 800 g and 850 g and two adult males, 1 450 g and 1 550 g) born in the laboratory, and one *Mustela lutreola* (adult female, body weight 700 g) which was live-trapped in a wooden-box trap in the southwest of France (D. P. N. authorisation 1995). Additionally, the author viewed a video on the locomotory behaviour of a *Mustela lutreola* male when it was released. The

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other animals were individually kept in 10 to 16 m^2 large open-air enclosures provided with a pool, a converted shed, and a resting place under normal photoperiod conditions. Food and water were supplied ad libitum.

The aquatic locomotory behaviour of the female mink and a polecat couple was studied in an open-air pool (2.0×1.5×0.9 m) with a transparent side. The second polecat couple was observed in a smaller pool (1.9×1.0×0.75 m). The water temperature was 20 to 21 °C, the outdoor temperature 19° to 24 °C. Visual marks were set along the transparent sides of both pools every 10 cm for measurements. Swimming behaviour was video-recorded with additional light and linear movement was timed to measure the progression speed. The number of swimming strokes was counted. The degree of body inclination was measured in relation to the horizontal axis. ALEXANDER (1982) proposed the calculation of the ratio between the length and the largest diameter of the body providing an indicative value for the resistance degree of body in the water. Thus, the ratio of the larger diameter of the body to its length (tail not included) was calculated in order to account for the drag resulting from movements.

Concerning terrestrial locomotion, the mink and one polecat couple were studied in a 3.8×3.6 m outside enclosure. The second polecat couple was studied in another outside enclosure (3.9×1.5 m). Only linear trajectories, walking or jumping, were taken into account in this study. The sequences were video-recorded (8 mm film) and timed to differentiate between walk and bounds (WILLIAMS 1983 b).

A progressive discriminant analysis was performed (PCSM program, D^2 of Mahanalobis) to assure differences in locomotion between the two species. The degree of freedom (df) depended on the number of experiments carried out.

Terrestrial locomotion: Walking was done as slow speed by *M. lutreola* (0.60 m/s, sd = 0.06) as well as *M. putorius* (female 0.61 m/s, sd = 0.06, males 0.62 m/s, sd = 0.07). No differences resulted between the females of both species (t = 0.13 df 34; $p > 0,9$), between the males (t = 0.88, df 29, $p > 0.5$), and also not between polecat males and females (t = 0.73, df 29, $p > 0.5$). Increase in speed led to a moving mode of bounds with a speed of 1.21 m/s (sd 0.12) for M. lutreola, 1.21 m/s (sd 0.10) for *M. putorius* females, and 1.23 m/s (sd 0.13) for males. No significant difference resulted (*M. lutreola* versus *M. putorius* females t = 0.14, df 24, $p > 0.9$, males t = 0.46, df 21, $p > 0.8$, polecat females versus males t = 0.37, df 21, $p > 0.7$).

Aquatic locomotion: The average swimming speed at the surface was 0.44 m/s (sd 0.03, n = 16) for *M. lutreola*, 0.42 m/s (sd 0.06, n = 16) for female polecats and 0.43 m/s (sd 0.04, n = 13) for males. The velocity did not differ between the females *M. lutreola* and *M. putorius* (t = 1.77, df 30, $p > 0.08$) and males (t = 0.63, df 23, $p > 0.6$), as well as male and female polecats (t = 0.89, df 18, $p > 0.4$). The four limbs were used alternatively during the propulsion although the hind limbs moved at a slower average rhythm (*M. lutreola* 2.70 strokes per sec. sd 026, female *M. putorius* 2.74 st/s sd 0.11, males *M. putorius* 2.81 st/s sd 0.12) with no significant differences (*M. lutreola* versus *M. putorius*, t = 0.51, df 20, $p > 0.4$; *M. lutreola* versus male *M. putorius* t = 0.97, df 15 $p > 0.3$; female versus male *M. putorius* t = 1.06, df 15, $p > 0.3$). The average rhythm of the forelimb movements was 3.50 st/s (sd 0.284) in *M. lutreola*, 3.64 st/s (sd 0.28) in *M. putorius* females and 3.80 st/s (sd 0.14) in *M. putorius* males. Also here, no significant differences occurred (*M. lutreola* versus *M. putorius* females t = 1.23, df = 27, $p > 0.2$; *M. lutreola* versus *M. putorius* males t = 1.96, df 17, $p > 0.8$, females versus males *M. putorius* t = 0.97, df 18, $p > 0.3$; Fig. 1).

The speed of motion was clearly correlated with the mean number of forelimb movements in both species (*M. lutreola* r = 0.650, df 12, $p < 0.012$; female *M. putorius* r = 0.602, $p < 0.018$, Fig. 2), whereas no correlation was ascertained between speed and the rhythm of hind limbs (*M. lutreola* r = 0.520, $p > 0.5$; *M. putorius* females r = 0.219, $p > 0.5$; *M. putorius* r = 0.433, $p > 0.5$). Most probably the propulsion is mainly dependent on fore-

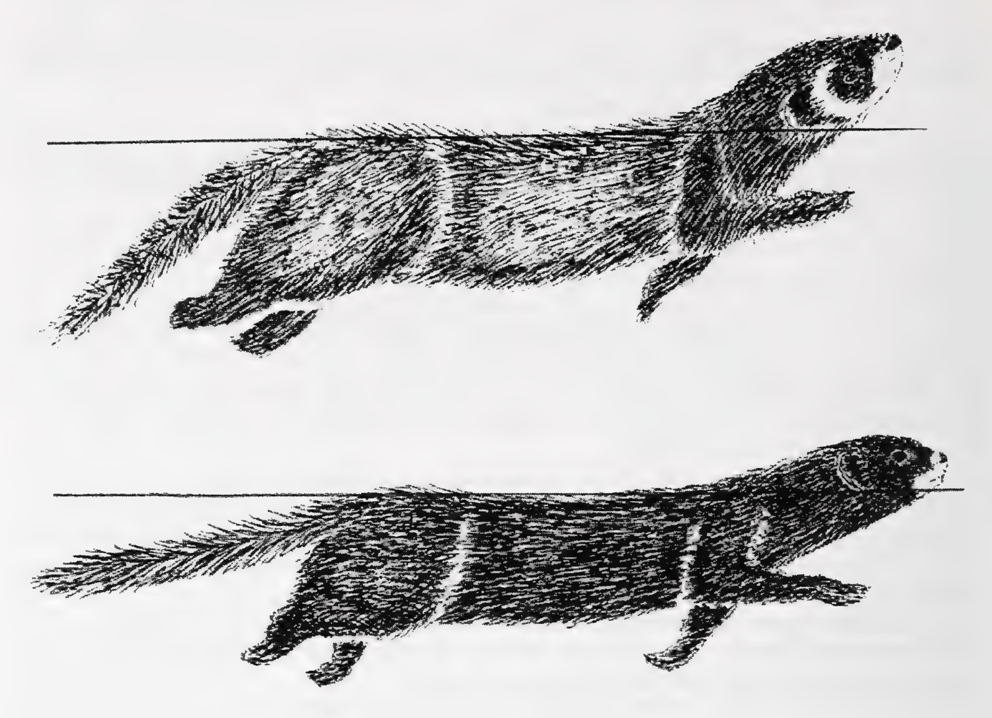


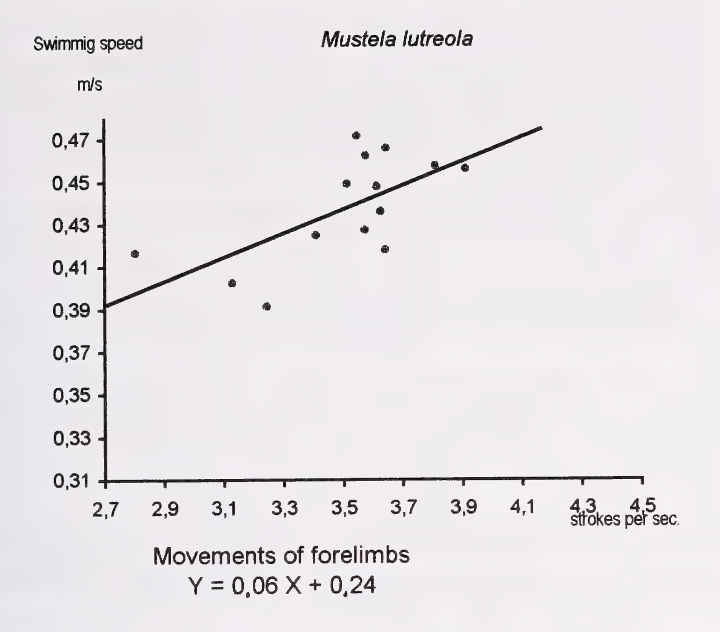
Fig. 1. The aquatic locomotory sequence: body inclination during swimming in *Mustela putorius* (top) and in *Mustela lutreola* (bottom).

limb movements. However, it was also interesting to note that in spite of a slower rhythm of forelimb movements during swimming, *M. lutreola* moved quicker than *M. putorius.* Thus, including "rhythm of forelimbs" as a co-variant, the variance analysis revealed a significant difference of velocity between *M. lutreola* and *M. putorius* females ($F = 6.84$, df 1,26, $p < 0.02$; parallelism difference $F = 2.51$, $p > 0.5$).

During swimming, the body position showed a mean inclination angle of 7°2′ (sd 2°8′, range = 2°5′–12°1′) for *M. lutreola.* This was significantly smaller ($t = 4.33$, df 28, $p < 0.001$) compared with *M. putorius* females (average 12°0′, sd 3°6′, range 6°3′–18°6′) or versus *M. putorius* males ($t = 3.59$, df 19, $p < 0.002$; average 12°1′, sd 2°2′, range 8°9′–15°7′). Concerning this degree of inclination, however, no difference occurred between females and males of *M. putorius* ($t = 0.04$, df 17, $p > 0.05$). The diameter to length ratio of the body was 0.11 in *M. lutreola*, 0.12 in *M. putorius* females and 0.12 in males. In both species, the head and body dorsum remained above water.

A further progressive discriminant analysis revealed that only the degree of inclination (Mahanalobis $D^2 = 2.12$, 100% increase, $p < 0.001$) contributed to distinguish significantly between the locomotory behaviours of both species. Swimming speed differed to a lesser extent ($D^2 = 2.54$, 19.9% increase, $p < 0.002$), walk ($D^2 = 2.63$, 3.7% increase, $p > 0.05$) and bounds ($D^2 = 2.64$, 0.4% increase, $p > 0.05$) not at all.

European mink and polecat differed only in their body position in the water, the mink showing a smaller degree of inclination. Terrestrial mammals often stand vertically in the water (LESSERTISSEUR and SABAN 1967). FISH (1993) noted also that the swimming behaviour was associated with a smaller inclination angle for the aquatic opossum *Chironectes* compared with terrestrial species. The quality of the fur improved floating (JOHANSEN 1962; LING 1970; DAGG and WINDSOR 1972) and the fur density in American mink was 780 per cm^2 (KUBY 1982). In *Mustela lutreola*, fur density reached about $600/cm^2$ and



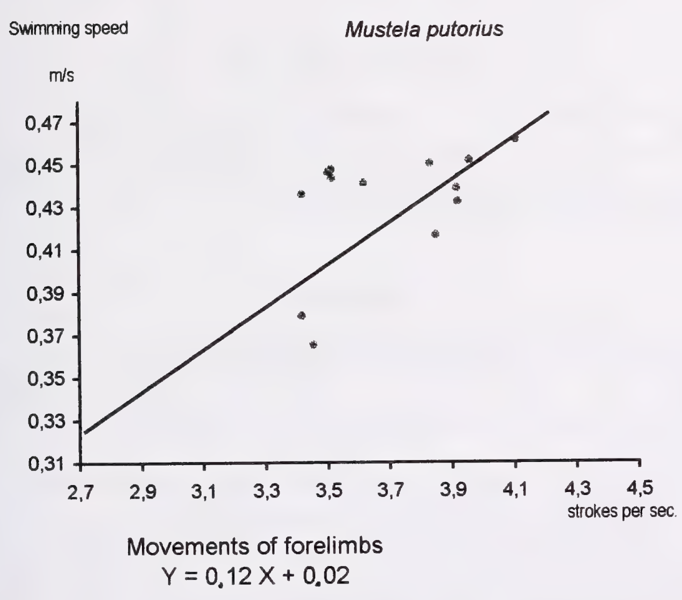


Fig. 2. Linear regression of swimming speed and mean number of forelimb movements in *Mustela lutreola* and *Mustela putorius.*

guard hair length averaged 23 mm, whereas fur density was only 300/cm^2 in polecat and guard hair length was up to 35 mm.

The European mink did not show ethological adaptations which were characteristic of species living in water habitat. Thus, the bipedal propulsion increased considerably the moving speed, and characterised the specialisation to the liquid element (Tarasoff et al. 1972; Fish 1984, 1993; Hildebrand 1989; Renous 1994). Furthermore, in the otter, the

undulations of the body perceptibly ameliorated moving speed (Tarasoff et al. 1972; Chanin 1985). In European mink and polecat, the aquatic locomotion was of a typical paraaxial mode and the propulsion was made by oscillatory movements in which the four limbs alternated. This pectoropelvic paddling was also noted in terrestrial carnivores (Alexander 1982; Braun and Reif 1985; Renous 1994). Swimming employing four limbs considerably affected the propulsion (Tarasoff et al. 1972; Fish 1984, 1993) and functioned at high metabolic cost (Williams 1983 a). The American mink showed a more efficient swimming behavior (from 0.46 m/s to 0.70 m/s, Poole and Dunstone 1976; Dunstone 1978; Williams 1983 a). Kuby (1982) observed that *Mustela vison* swam mainly with an alternating movement of forelimbs, only occasionally using the hind limbs, Kruska and Kuby (pers. comm.) noted that forelimbs were used about twice as fast compared with hindlimbs.

In mustelids, walk consisted of a symmetrical gait in which the forelimb took off after the hindlimb from the same body side (Goethe 1964). Terrestrial mobility did not differ between European mink and polecat and the speed increase was associated with an adaptation of the locomotory behaviour, namely bounds (Goethe 1964; Williams 1983 b). The slow walk constituted the characteristic gait of the foraging behaviour in polecat (Weber 1989; Lodé 1993, 1994) and this type of locomotion mainly improved the olfactory search for food (Wüstehube 1960; Weber 1989). In fact, the locomotory behaviour of the European mink differed very slightly from the polecat and consequently, could only partially reply to the constraints imposed by the exploitation of freshwater habitat.

Acknowledgements

This work is part of the program on the study and protection of endangered western populations of *Mustela lutreola*. I would like to thank especially P. Garguil, O. Grosselet, M. Guérineau, V. Herrenschmidt, D. Le Jacques, V. Luyen, and C. Maizeret. I also thank Prof. Dr. D. Kruska for his helpful comments.

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Z. Säugetierkunde **64** (1999) 116–120
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Distribution and habitat of selected carnivores (Herpestidae, Mustelidae, Viverridae) in the rainforests of southeastern Nigeria

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Receipt of Ms. 15. 09. 1998
Acceptance of Ms. 14. 01. 1999

Key words: Herpestidae, Mustelidae, Viverridae, habitat, Nigeria

Nearly all the small – to medium – sized carnivorous mammals (Herpestidae, Mustelidae, and Viverridae) living in West Africa, including southeastern Nigeria, are threatened by uncontrolled hunting activities (POLITANO 1997). This continued hunting activity has provoked a severe effect on the status and population abundance of several species, including those which are especially relevant in the biogeographic or conservation point of view. A recent field investigation in the eastern Niger Delta (Port Harcourt, Rivers State, Nigeria, see POLITANO 1997) has permitted to obtain records for twelve species. Another species (*Genetta thierryi*), a typical inhabitant of Guinea savannas (KINGDON 1997), may possibly be present in the study area, but no actual data about its presence have been collected (POLITANO 1997).

During recent years, an increased interest has arisen on the distribution and status of small- and medium-sized carnivores of southeastern Nigeria (HEARD and VAN ROMPAEY 1990; POWELL 1997; SINGH et al. 1995). In this study we therefore report novel data on the status of several selected species of Herpestidae, Mustelidae, and Viverridae, and on their distribution and the habitat frequented.

The research study was conducted during five field expeditions (for a total of 213 days in the field) between September 1996 and May 1998 in four regions of southeastern Nigeria (see Fig. 1): eastern Niger Delta (Port Harcourt region, Rivers State, approx. 04°45′ N, 07°01′ E), region of Aba (Abia State, 04°47′ N, 07°35′ E), region of Eket (Akwa-Ibom State, 04°50′ N, 07°59′ E), and region of Calabar (Cross River State, 04°48′ N, 08°21′ E). These areas, which are heavily populated with hundreds of villages interspersed by patches of forests and cultivated lands, are especially important for the economy of Nigeria because of the extensive oil extraction and liquefied natural gas transmission installations. The forest patches may be dryland or of the swamp rainforest type. Mangrove forests (*Avicennia* ssp., *Rhizophora racemosa*) are the dominant types of vegetation in the areas of the fluvial systems influenced by salt-water or brackish-water. The climate of the study regions is tropical sub-Saharan, with well-marked dry and wet seasons and relatively little monthly fluctuations in maximum and minimum temperatures (GRIFFITHS 1972).

Data given here were collected by means of the following methods: (i) specimens shot and trapped by hunters accompanied by the authors; (ii) specimens examined in small village markets of local tribes (for the methodology employed, cf. AKANI et al. 1998); (iii) field observations performed by us during the expeditions for assessing the environmental impact of the "LNG Natural Gas Liquefied and Transmission System" by the company

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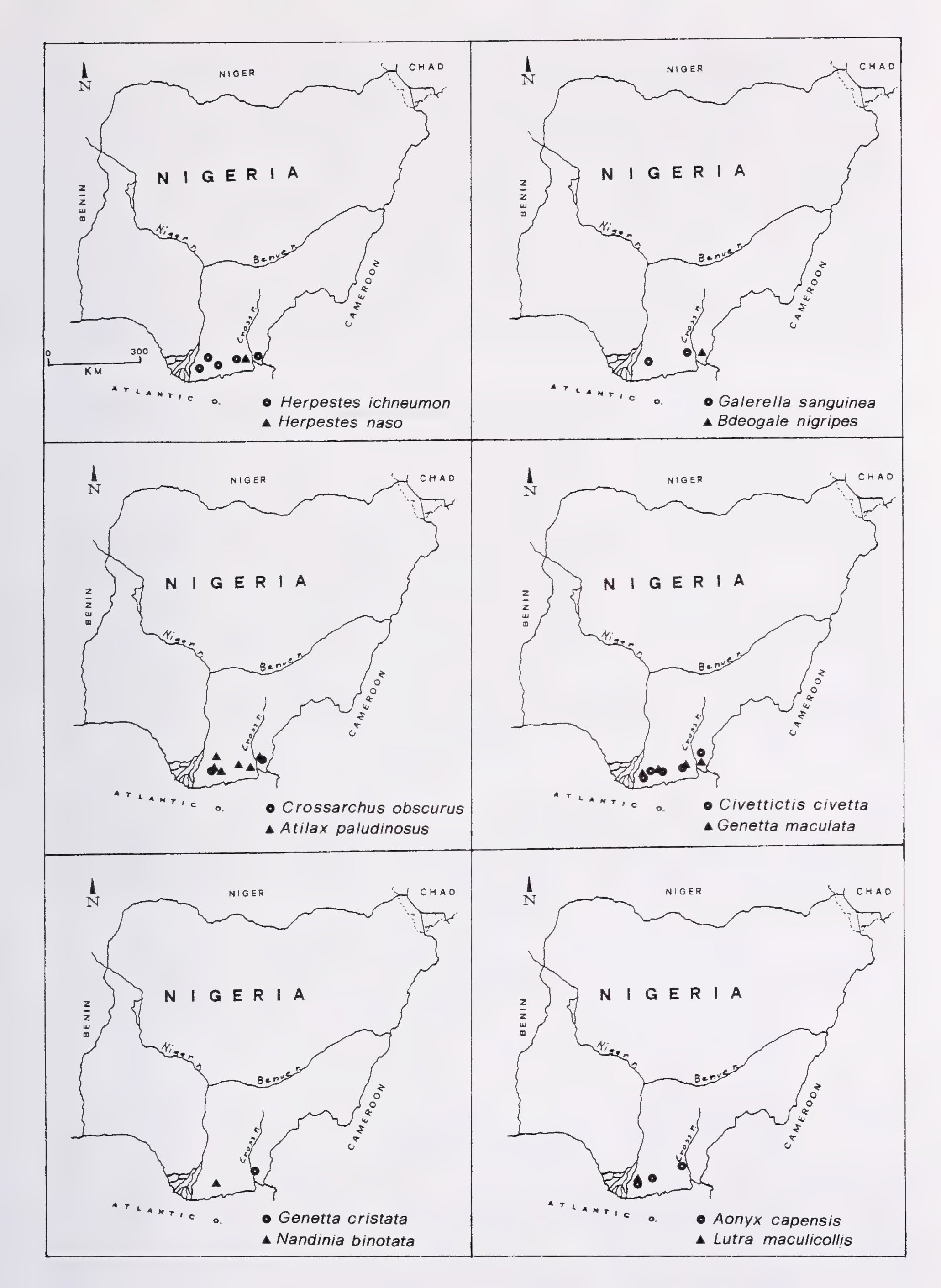


Fig. 1. Map of Nigeria, showing the distribution records relative to the various species studied.

"T.S.K.J. Nigeria Ltd." (Politano 1997), and (iv) skulls, remains, tracks, and other signs of the presence of the various species in the field.

Systematics of several taxa (e. g. those belonging to the genus *Genetta*) is still far from being well understood. Thus, for practical reasons, we followed Wozencraft's (1993) indications, apart for the fact that we recognize as a valid species *Genetta cristata* (Rosevear 1974; Crawford-Cabral 1981).

We subdivided the available habitat types into seven categories: (1) primary dryland forest, (2) secondary dryland forest, (3) former cultivations recolonized by bushy vegetation ("bush"), (4) swamp-forest, (5) mangroves, (6) farmlands and cultivated lands, and (7) aquatic environment (river banks, lakes, creeks, estuarine habitat, etc).

In total, we recorded 122 carnivore specimens. *Herpestes ichneumon*, *Atilax paludinosus*, *Civettictis civetta*, and *Genetta maculata* were the more frequently encountered taxa (Tab. 1).

The habitat of observation of each carnivore specimen recorded during the present study is presented in table 1. Pooling all the studied species, the higher amount of observation (30.3 % of the total, n = 122) was done in habitat (3), but many observations were done even in habitat (6) (22.1 %) and in habitat (2) (18 %). Conversely, only a few observations were done in all the other habitat categories. Records of distribution relative to the study species are presented in figure 1. With regard to *H. ichneumon*, it is somewhat surprising that this species was said to be a newly reported taxon for the Niger Delta by Powell (1997), since it was discovered in bush-meat markets of Imo and Rivers States by Ojonugwa (1986). Indeed, our data indicate that *H. ichneumon* is one of the most commonly hunted Herpestidae by Niger Delta tribes. *Herpestes naso* was recorded west of Cross River, thus confirming Powell (1997). *Galerella sanguinea*, previously recorded in northern and drier sites (Happold 1987), was shown to have penetrated in southern-more sites within the Niger Delta into wetter areas. *Bdeogale nigripes* was recorded only east of Cross River, but we cannot exclude that it is also present west of this river. *Cross-*

Table 1. Numbers of specimens observed and their relative habitat of observation, of several species of Herpestidae, Viverridae, and Mustelidae found in the study regions of southeastern Nigeria. Habitat types: (1) primary rainforest, (2) secondary rainforest, (3) former cultivations recolonized by bushy vegetation ("bush"), (4) swamp-forest, (5) mangroves, (6) farmlands and cultivated lands, and (7) aquatic environment (river banks, lakes, creeks, estuarine habitat).

Species	(1)	(2)	(3)	(4)	(5)	(6)	(7)
HERPESTIDAE							
Herpestes ichneumon		4	13			12	
Herpestes naso						1	
Galerella sanguinea		1	2			2	
Bdeogale nigripes	1						
Crossarchus obscurus	1	1					
Atilax paludinosus		2		18			9
VIVERRIDAE							
Civettictis civetta		6	14			7	
Genetta maculata	3	7	8			4	
Genetta cristata		1					
Nandinia binotata						1	
MUSTELIDAE							
Aonyx capensis							3
Lutra maculicollis							1

archus obscurus and *A. paludinosus* are widespread throughout the study area but the former is probably rarer. The same is true for *C. civetta* and *G. maculata*, which are widespread throughout the study area. With respect to *G. cristata*, possibly the most important viverrid species in south-eastern Nigeria because of its rarity and unknown biology (cf. HEARD and VAN ROMPAEY 1990), we were able to collect only one recent record from a bush-meat market in Itu (Cross River State). The hunter collected this specimen from a secondary forest patch situated in the surroundings of Itu, whereas HEARD and VAN ROMPAEY (1990) recorded this species from other areas of Cross River State, practically contiguous to the our own (e.g. Akampka, Oban, etc). In any case, POWELL (1997) recorded it even from the west side of this river. The status of this species is still unknown, because the problems of correct identification of various species of the genus *Genetta* by local people (including experienced hunters) causes strong problems in obtaining a reliable data-set (ROSEVEAR 1974; SCHLAWE 1981; HAPPOLD 1987; WOZENCRAFT 1993; KINGDON 1997).

Nandinia binotata is widespread in the study area (HAPPOLD 1987; KINGDON 1997; STUART and STUART 1997), but we recorded it just once during our surveys. Probably this rarity in our records depended on its arboreal habits, thus making this species rarely prey to human hunters; in fact, it is rarely captured by ground traps. In agreement with POWELL (1997), we confirmed the presence of *Aonyx capensis* and *Lutra maculicollis* for the study region. Considering the wide extension of the fluvial systems, creeks, and water bodies, we are led to believe that the apparent rarity of the otter species is in fact exaggerated, given the extremely elusive habits of these semi-aquatic carnivores. Otters are certainly present along the Upper Orashi River Course (at least from the village Elem-Sangama) and in other freshwater river tracts characterized by rainforest patches along the banks.

Our surveys demonstrated that there is still a remarkable diversity of small- and medium-sized carnivores in southeastern Nigeria, despite the strong alteration of the natural environment of this African region. The fact that many records were relative to bushy and cultivated lands suggests that these species are now well adapted to the environments modified by humans. There was a lack of data from mangrove forests. It is likely that this depends on the fact that this habitat type is very unfavourable to these animals. This habitat is deficient in available prey type to support stable populations of carnivores. For instance, frogs and toads, which are components of the diet of several carnivores (e.g. *A. paludinosus*, ROSEVEAR 1974), are nearly completely absent from brackish water river tracts where mangroves grow up (POLITANO 1997).

It is suggested that Cross River is a main barrier for many animal species, including mammals (HAPPOLD 1987; KINGDON 1989, 1997). However, this is not likely to be true for medium-sized carnivores, this being demonstrated by the recent records relative to several species west of the Cross River by POWELL (1997) and the present study.

Acknowledgements

We are indebted to the companies 'T.S.K.J. Nigeria Ltd.' (Port Harcourt and Lagos), 'Ecosystem s.r.l.' (Bari), 'Aquater s.p.a.' (San Lorenzo in Campo), and 'Amertex Oil and Gas Ltd.' (Lagos) for supporting parts of our research in Nigeria. Special thanks go to P. M. AKANIWOH for having indicated some remarkable sites for observing carnivore tracks and signs. Several hunters provided us with original records on their trapped animals. Finally, we thank particularly Dr. E. E. NYONG (Governor of Cross River State), and Dr. E. M. BOCO (Chief of Calabar) for providing security assistance. Two anonymous referees considerably improved an earlier draft of the manuscript.

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Z. Säugetierkunde **64** (1999) 121–125
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

The occurrence and biogeographic significance of the southern Spiny pocket mouse *Heteromys australis* in Venezuela

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Receipt of Ms. 21. 09. 1998
Acceptance of Ms. 27. 11. 1998

Key words: *Heteromys*, spiny pocket mice, biogeography, Andes, Venezuela

Although the origin and center of diversity of the rodent family Heteromyidae (spiny pocket mice and relatives) lie in North or Central America (Rogers 1990), two species of *Heteromys* are known to inhabit northwestern South America *Heteromys anomalus (*Thompson, 1815) is distributed across northern Venezuela and Colombia and in the Río Magdalena Valley of central Colombia. *Heteromys australis* Thomas, 1901 is known only from northwestern Ecuador north through western Colombia to eastern Panama and east through the Colombian Andes to near Bogotá (Williams et al. 1993).

We herein report a specimen of *Heteromys australis* from the Cordillera de Mérida in northwestern Venezuela, extending the distribution of this species ca. 350 km to the northeast across the Depresión del Táchira. At present, the nearest museum records of *H. australis* are from the western slopes of the Cordillera Oriental in Colombia. The specimen is an adult female (CVULA I-3503), consisting of a skin, skull, and partial post-cranial skeleton from Presa La Honda, 10 km SSE Pregonero, Estado Táchira, at 1 100 m. Ochoa and Soriano (1991) previously reported this individual as *H. anomalus* based on distribution.

To confirm the species identity, we compare this individual with Venezuelan specimens of *H. anomalus* and with *H. australis* from the eastern extent of its range in Colombia. Dental and pelage criteria for age classification of specimens follow Rogers and Schmidly (1982), as do cranial measurements (Tab. 1). The following specimens form the basis for our comparisons. Museum abbreviations follow Hafner et al. (1997) when available: Colección de Vertebrados de la Universidad de los Andes, Mérida (CVULA), The Field Museum, Chicago (FMNH), Instituto de Ciencias Naturales, Bogotá (ICN), and Museo del Instituto La Salle, Bogotá (MLS).

Specimens Examined – *Heteromys anomalus* (64): Venezuela: Estado Barinas, Barinitas (1, CVULA I-2329), Barragán-Barinitas, 400–440 m (3, CVULA I-837, 904, 1161), Cerro Alto, 3 km N La Soledad, 1 500–1 580 m (13, CVULA I-846, 924, 926, 1037, 1040-2, 1044-8, 1294), Cerro Alto, 2 km NW La Soledad, 1 460–1 600 m (3, CVULA I-5924, 5932, 5939), El Palmar, N Barinitas, 1 000 m (1, CVULA I-1049), Hacienda Las Matas, 40 km SE Barinas, 270 m (4, CVULA I-4015, 4048, 4297, 4346); Estado Lara, El Blanquito, P.N. Yacambú, 9 km SE Sanare, 1 600 m (10, CVULA I-2695, 2728, 2732, 2736, 2741-3, 2750, 2754-5), El Blanquito, P.N. Yacambú, 17 km SE Sanare, 1 600 m (1, CVULA I-6162); Estado Mérida, Bejuquero, W Zea, 600 m (2, CVULA I-256-7), Capazón, La Azulita, 1 000 m (4, CVULA I-1038-9, 1043, 1047), Cucuchica, 6 km E Tovar, 1 200–1 250 m (10, CVULA I-5971, 5986-8, 5993, 6003-4, 6008-9, 6019), El Vigía, Hacienda El

0044-3468/99/64/02 – 121 $ 12.00/0

Table 1. External and cranial measurements (mm) for *Heteromys* of age classes 3 and 4 (Rogers and Schmidly 1982) from selected localities in Colombia and Venezuela. See text for exact localities and specimen numbers. Means plus or minus standard errors are given, followed by sample sizes. The sample of *H. australis* from Pregonero represents the single specimen of that species known from Venezuela (CVULA I-3503).

	H. australis: Huila, Río Suaza (Colombia)	*H. australis:* Táchira, Pregonero (Venezuela)	*H. anomalus:* Barinas, Cerro Alto (Venezuela)
Total length	274.2 ± 7.82, 12	268	290.0 ± 8.82, 6
Tail length	149.0 ± 3.14, 12	152	160.2 ± 6.80, 6
Hind foot length	33.7 ± 0.31, 12	34	35.8 ± 0.40, 6
Ear length	17.5 ± 0.26, 12	19	19.0 ± 0.58, 6
Greatest skull length	34.6 ± 0.33, 7	32.7	35.9 ± 0.60, 2
Zygomatic breadth	16.3 ± 0.16, 8	n/a	17.2 ± 0.34, 3
Rostral length	15.1 ± 0.30, 9	13.7	15.4 ± 0.31, 3
Nasal length	13.5 ± 0.21, 9	13.0	13.8 ± 0.15, 3
Least interorbital constriction	8.3 ± 0.10, 10	7.5	8.5 ± 0.15, 6
Mastoid breadth	15.0 ± 0.08, 6	14.8	15.7 ± 0.25, 4
Maxillary toothrow length	5.2 ± 0.06, 11	5.4	5.6 ± 0.13, 6
Interparietal width	8.4 ± 0.14, 7	9.1	9.3 ± 0.15, 3
Interparietal length	4.6 ± 0.12, 6	5.4	5.0 ± 0.12, 3
Skull depth	10.9 ± 0.14, 7	10.7	11.2 ± 0.19, 4

Roble, 150 m (1, CVULA I-894), Finca Mesa Rica, Cucuchica, 8 km W Tovar, 1 250 m (1, CVULA I-6024), Hacienda La Trinidad, Caño Tigre, 370 m (2, CVULA I-2528-9), La Cuchilla del Niño, 2 km SW Zea, 1 250 m (1, CVULA I-6021); Estado Táchira, San Pedro del Río, 12 km W Michelena (1, CVULA I-6196), Río Potosí, Uribante, 1 050 m (1, CVULA I-2516); Estado Trujillo, Macizo de Guaramacal, 6 km SE Boconó, 2 430 m (1, CVULA I-2960); Estado Zulia, El Tucuco, 46 km SSW Machiques, 300–400 m (2, CVULA I-1890, 5698), Río Arajamo, Sierra de Perijá, 1 000 m (2, CVULA I-1507-8). *Heteromys australis* (20): Colombia: Departamento de Boyacá, Serranía Las Quinchas, Puerto Boyacá, 1 175 m (2, ICN 13150-1); Departamento de Cundinamarca, Paime (1, MLS skin #2303); Departamento del Huila, Río Suaza Río Aguas Claras, near San Adolfo, 1 400 m (16, FMNH 71191–71206). Venezuela: Estado Táchira, Presa La Honda, 10 km SSE Pregonero, 1 100 m (1, CVULA I-3503).

The specimen of *H. australis* from Pregonero (CVULA I-3503) is a young adult female in the process of molting into adult pelage. The permanent premolars are well worn, and the lophs of most upper molars form a u-shaped crown pattern, placing it between age classes III and IV of Rogers and Schmidly (1982). Externally, it displays the dark, slaty black dorsal pelage characteristic of *H. australis* with only the slightest grizzling of ochraceous hairs, in contrast to the usually brownish, more grizzled dorsum of *H. anomalus*. The tail is only indistinctly bicolored, with some dark hairs present on its ventral surface, as in *H. australis*, and is much shorter than those of *H. anomalus* (Tab. 1).

Cranially, the Venezuelan specimen agrees with *H. australis* in its relatively wider and absolutely shorter skull than *H. anomalus*, which have more elongated skulls. It also presents the wide, inflated braincase characteristic of *H. australis* (Williams et al. 1993). The rostrum is narrower and, although the zygomatic arches are broken, the anterior roots of the zygomatic arch are clearly more gracile than in *H. anomalus*. The masseteric fossa is only shallowly excavated in Venezuelan and Colombian specimens of *H. australis*, whereas that of *H. anomalus* is deeply excavated. These characters hold up for all within-age-class comparisons for age classes III and older.

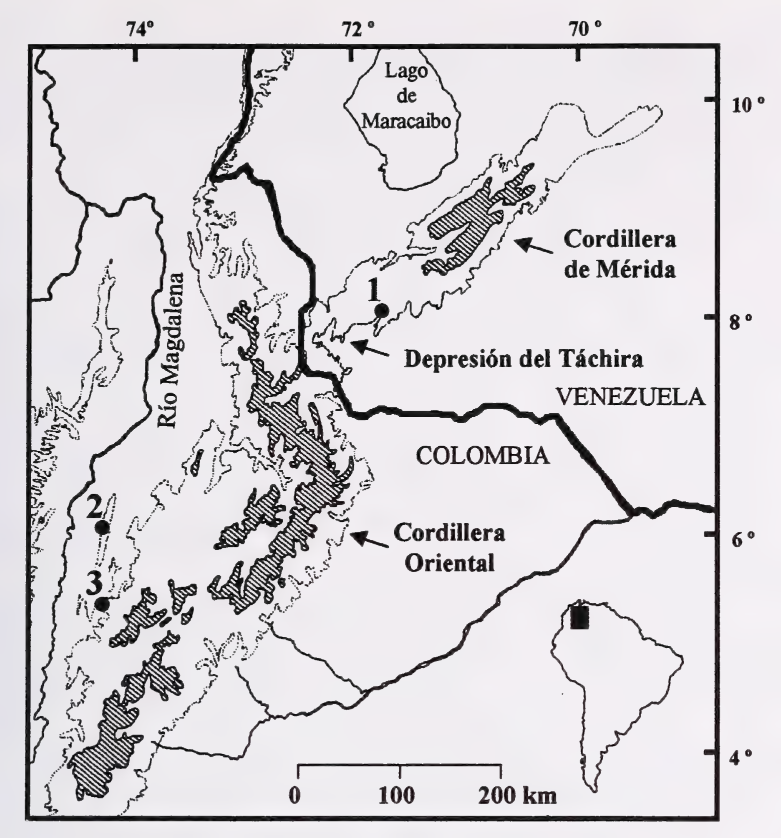


Fig. 1. Map showing the known collection localities of *Heteromys australis* in the eastern extent of its range in Venezuela and Colombia. The species continues its distribution to the west in Colombia, Ecuador, and Panama. The 1 000 m contour is marked by a dotted line, and areas over 3 000 m are stippled. 1) = Pregonero, Táchira; 2) = Serranía Las Quinchas, Boyacá; 3) = Paime, Cundinamarca. See text for exact localities and specimen numbers.

This range extension places *H. australis* to the east of the Depresión del Táchira, an area of low hills and ridges which separates the Cordillera de Mérida from the Cordillera Oriental of the Andes (Fig. 1) and which constitutes an important zoogeographic barrier (Soriano et al. 1999). Whereas *H. anomalus* tolerates a wide precipitation range, *H. australis* is found only in wet lowland and montane forests. Thus, the present habitat in the Depresión del Táchira is likely too xeric for *H. australis.* We hypothesize that *H. australis* probably colonized the Pregonero area during a past glacial period and that its present-day occurrence there represents a relict population disjunct from populations in the Cordillera Oriental.

Heteromys australis is likely present at middle elevations elsewhere in the southern portion of the Cordillera de Mérida (where it occurs in close parapatry with *H. anomalus* – note CVULA I-2516), and may eventually also be found on the eastern slopes of the Cordillera Oriental. The specimen from Pregonero has a much thinner alisphenoid strut and a more constricted interorbit than Colombian specimens of the same species. Hence, this Venezuelan population of *H. australis* may be slightly differentiated from the more western populations. However, at this time, we do not recognize it as subspecifically distinct on the basis of a single specimen.

The range retraction and subsequent isolation we hypothesize for *H. australis* parallel the distributional patterns of other montane taxa in the region. Cuatrecasas (1986) illustrated probable distributions of the rosette "frailejones" of the plant genus *Espeletia* (Asteraceae), uninterrupted through the wet páramos of the northern Andes during the latter part of the Last Glacial, in contrast to the present, fragmented distribution of the genus. Similarly, Lynch (1986) presented a phylogeny and distributional map for the monophyletic *Eleutherodactylus devillei* assembly, five species of leaf litter frogs restricted to cloud forests and subpáramo habitats in the northern Andes. In that system, *E. briceni*, from the Mérida Andes, is the most basal member of the clade, presumably the first to undergo a vicariant separation from the ancestral populations to the southwest and undergo speciation.

Given the North or Central American origin of heteromyids, populations of *H. australis* probably only have experienced one or a few Pleistocene glacial cycles in the region, whereas these other groups have a long history in the Andes. If the range disjunction identified for *H. australis* originated with Pleistocene glacial bouts, as argued here, then such a pattern provides evidence that the species was already present in South America before the Holocene. This suggestion counters Marshall et al. (1982), who assumed a Recent dispersal of heteromyines into South America based on the lack of a fossil record for the group. Rather, it is compatible with Rogers' (1990) biochemical evidence that suggested a relatively old origin of the *H. anomalus* and *H. australis* groups, long before the end of the last glaciation.

Other unexpected mammals have been collected at Pregonero as well, indicating the area's possible biogeographic importance. The aquatic rat *Neusticomys mussoi* is known only from its type locality near Pregonero (Ochoa and Soriano 1991). In addition, the short-tailed opossum *Monodelphis adusta* was first reported for Venezuela from this locality (Soriano 1987), but subsequently has been found near Zea on the northern-facing slopes of the Cordillera de Mérida (Ramoni-Perazzi et al. 1994). The only known specimens of the phyllostomid bat *Sturnira tildae* in the Cordillera de Mérida also were collected in Táchira near Pregonero (Ochoa et al. 1993). The fauna of this part of the Cordillera, the Río Uribante drainage, may share greater similarity with that of the Colombian Andes than with the rest of the Cordillera de Mérida. However, the scarcity of collections from similar elevations elsewhere in the Cordillera de Mérida precludes definitive conclusions regarding general distributional patterns of these small mammals.

Acknowledgements

We thank the following curators for access to specimens under their care: Alberto Cadena (ICN), Hermano Roque Casallas and Arturo Rodríguez (MLS), and Bruce D. Patterson (FMNH). The manuscript benefited greatly from careful comments offered by Michael D. Carleton, Marcela Gómez-Laverde, A. Townsend Peterson, Duke S. Rogers, Norman A. Slade, and Robert M. Timm. This work was partially funded by the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICIT) and the Consejo de Desarrollo Científico, Humanístico y Tecnológico de la Universidad de los Andes (CDCHT-ULA) through the grants RP-VII-240056 and C-564-92-01-A, respectively. Anderson's research on *Heteromys* was supported by a National Science Foundation Graduate Fellowship, a Fulbright Fellowship (Colombia-USA), and by grants from the E. Raymond Hall Fund (KUNHM Mammal Division) and the Thomas J. Dee Fund (FMNH).

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Z. Säugetierkunde **64** (1999) 126–127
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On the karyotype of the Long-clawed mole vole, *Prometheomys schaposchnikovi* Satunin, 1901 (Mammalia: Rodentia), in Turkey

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Receipt of Ms. 07. 04. 1998
Acceptance of Ms. 20. 11. 1998

Key words: *Prometheomys schaposchnikovi, karyology, Turkey.*

Satunin (1901) described *Prometheomys schaposchnikovi* from Gudaur (Georgia), examining a male specimen. Vinogradov and Argyropulo (1941), and Ognev (1948) recorded this species from various localities in Caucasia. Spitzenberger and Steiner (1964) gave the first record of *P. schaposchnikovi* from Turkey. The aim of this study is to contribute to karyological characteristics of *P. schaposchnikovi*.

We collected 19 specimes from two localities (Fig. 1) (Kutul plateau of Ardanuç 7, and Ardahan 12). Five specimens from Kutul (n = 2) and Ardahan (n = 3) were karyotyped based on the technique of Ford and Hamerton (1956).

The diploid number of chromosomes is 2n = 56, the number of autosomal arms is NFa = 100, and the fundamental number is NF = 104. The autosomal set consists of 12 metacentrics, 34 subtelocentrics, and 8 acrocentrics. The X chromosome is a large submetacentric, and the Y chromosome is the smallest metacentric (Fig. 2).

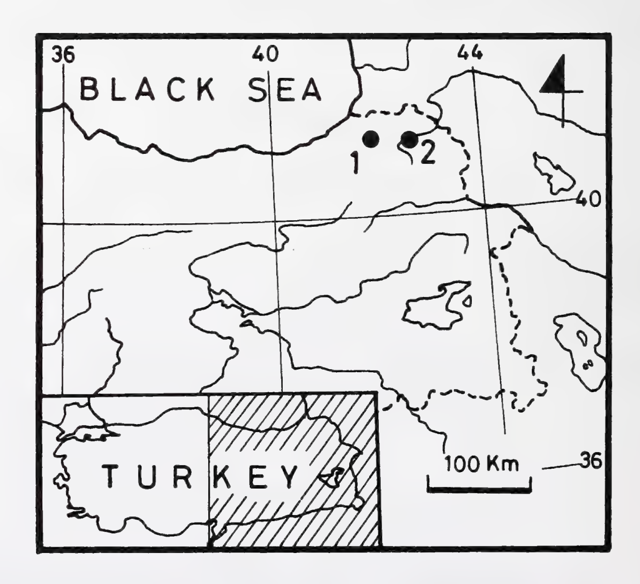


Fig. 1. Recorded localities (●) of *P. schaposchnikovi*. 1. Ardanuç 2. Ardahan.

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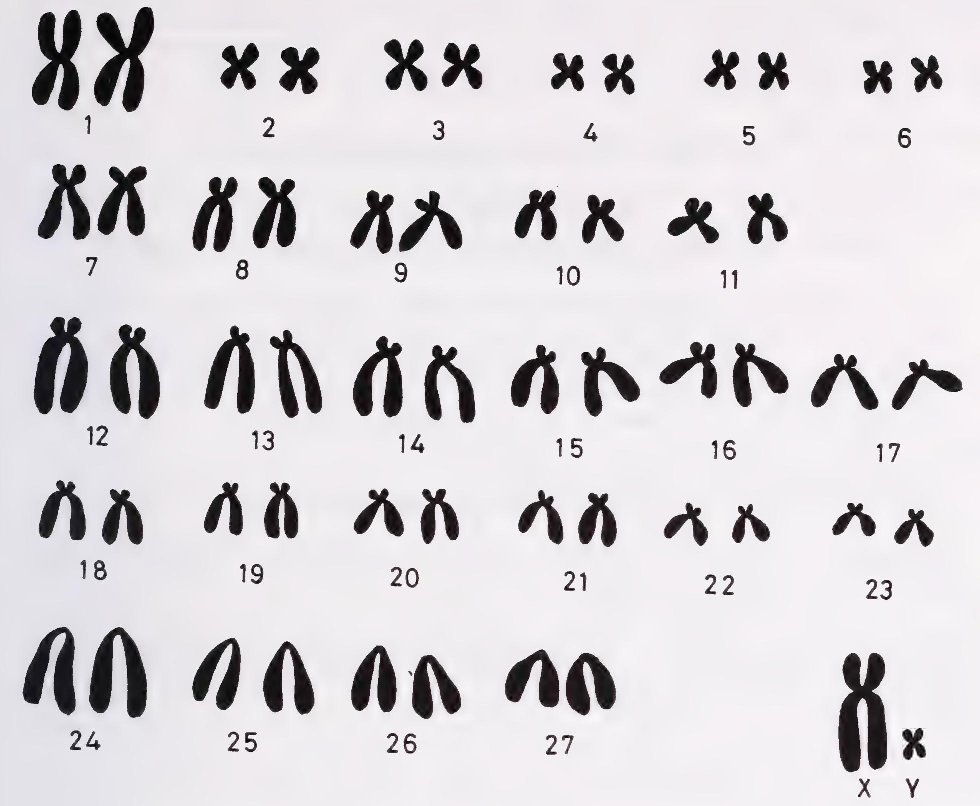


Fig. 2. Karyotype of a male *P. schaposchnikovi* from Ardahan.

According to Zima and Kral (1984), NFa is 70 and the Y chromosome is the smallest acrocentric, whereas in Turkish population the NFa is 100 and the Y chromosome is the smallest metacentric. Matthey (1958) described the karyotype of this species from Caucasia. We examined a metaphase plate from his publication and found that it is similar to that of Turkish specimens.

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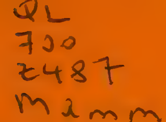
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



ISSN 0044-3468 · Z. Säugetierkunde · 64(1999)3 · S. 129-192 · Juni 1999

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Kinematic analysis of treadmill locomotion of Tree shrews, *Tupaia glis* (Scandentia: Tupaiidae)

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Receipt of Ms. 05. 08. 1998
Acceptance of Ms. 28. 12. 1998

Abstract

The cineradiographic analysis of the treadmill locomotion of tree shrews, *Tupaia glis* comprises walk, trot, and gallop. At symmetrical gaits, *T. glis* accelerates primarily by increasing step frequency but at gallop, step length is increased by including a suspension period. During all gaits, the site of foot down is directly below the eye. The femur is in horizontal orientation at foot down, at lift off humerus and tibia are parallel to the ground. At the end of the stance phase elbow and knee joint are more extended during symmetrical gaits than at gallop (30–40°). Biphasic shoulder joint movements observable during symmetrical gaits are reduced to monophasic movements at gallop. The onsets of flexion and extension movements are mostly before foot down and lift off. Body propulsion is mainly achieved by action of the proximal limb segments (scapula: 42–43 % during all gaits, 'pelvic movement': 42 % at gallop). For the first time, kinematics of the intervertebral thoracic and lumbar joints were calculated from X-ray films. Additive sagittal spine movements occur in the caudad thoracic and lumbar intervertebral joints and contribute substantially to body propulsion. The analysed kinematic and metric parameters of *T. glis* are common in mammals of small to medium size and seem to be independent of the taxonomic group of the animal.

Key words: *Tupaia glis*, cineradiography, kinematics, spine movement

Introduction

Tupaia glis is a small squirrel-like mammal which lives in the tropical and subtropical rain forest of southeast Asia. Tupaiidae are often considered to be a sister group of Primates (Novacek 1992). The most recent common ancestor of primates and tupaias could have been similar to modern tree shrews as far as anatomy, life history, and locomotion are concerned. Therefore, *Tupaia* could be a "possible 'model' of a primitive primate or placental mammal" (Jenkins 1974 a). This idea led to many studies on various aspects of tupaiid biology, including the first cineradiographic investigations on therian locomotion (Jenkins 1971, 1974 a). Jenkins (1974 a) paid special attention to spinal movements and found the region of greatest sagittal mobility to be located between the four vertebrae Th 11–L1. No movements were observed in the lumbar spine.

The observations of Jenkins (1971, 1974 a) were partly in contradiction to our studies on other therian mammals of the same or slightly larger size. We began a series of studies

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that centered around the kinematics of taxonomically and morphologically very different small to medium sized mammals. (FISCHER 1994; KÜHNAPFEL 1996; FISCHER and LEHMANN 1998; SCHMIDT and FISCHER 1999). A striking feature in the locomotion of all these mammals was the additive sagittal movement of the lumbar spine during in-phase gaits. Furthermore, body propulsion was mainly achieved by actions of proximal limb segments such as scapula movements.

In this study, the kinematics of fore- and hindlimbs, as well as movements of the complete thoracic and lumbar vertebral column were quantitatively analysed in animals that ran on a treadmill. Kinematics describe the relative orientation of limb segments during a step cycle. It comprise the angular movements in their amplitude and effective contribution to linear step parameters, joint and segment angles at the beginning and the end of stance and swing phase, as well as the intralimb coordination of joint movements. We distinguish between the caudal or cranial rotations of limb segments (i. e., retro- and anteversion, respectively) and the movements of the joints proper. We describe the angles relevant for propulsion in their projection onto the sagittal plane. The kinematics of the intervertebral thoracic and lumbar joints were calculated from X-ray films.

We are especially intrigued about the locomotion of *Tupaia* because of its postulated similarity with, firstly, the most common recent ancestor of primates and, secondly, with that of all placental mammals. In this context the question arises as to whether the characteristics of tupaiid locomotion are strictly size related or show some traits that point to its supposed relationships with primates. We build upon the work of JENKINS, however, our own work on various other mammals showed that a more detailed approach is necessary to address these questions.

Material and methods

Experiments were performed on adult *Tupaia glis*. Only two animals (male 210 g, young female 151 g) could be trained by positive conditioning to move on a horizontal motordriven treadmill within a Perspex® enclosure (100 cm × 45 cm × 11 cm). Tread speed was not fixed, but held manually at a relative constant level during X-ray shots. Only cineradiography allows to track skeletal movements, particularly of the proximal segments, i. e. scapula, humerus, pelvic, and femur. The cineradiographic films were made in several sessions at the Institut für den wissenschaftlichen Film (IWF) at Göttingen. The X-ray system consists of an automatic Phillips® unit with one X-ray source image amplifier chain. Pulsed X-ray shots were applied (50 kV, 200 mA). Films were exposed at 150 frames/s. The animals were filmed in a lateral projection. They were placed as closely to the image amplifier as possible (10 cm) and at maximum distance from the X-ray source (1 m), in order to reduce optical distortions. The images were taken from the image amplifier using a Arritechno® R 35–150 camera. Fore- and hindlimbs were filmed separately because the animal was longer than the X-ray screen (20 cm). An orthogonal grid perpendicular to the projection plane provided reference points for motion analysis and correction of geometrical distortions. The animals were filmed synchronously with two video cameras (50 Hz) in lateral and dorsal views. X-ray films were copied to video tapes (VHS).

In spite of several months of habituation, the tupaias did not perform all possible gaits. The animals did not show bounds on the treadmill. Therefore, only the symmetrical gaits such as walk and trot, as well as gallop were studied. Out of the filmed sequences, for a frame-by-frame analysis only those runs with continuous motion of the animals were selected. The cineradiographic tapes were A–D converted with a video processing board (Screen Machine® I, Fast® Multimedia AG, Munich, Germany). We further processed the frames by using a software that was written for this specific purpose ('Unimark' by R. Voss). It allows to digitize interactively previously defined landmarks with a cursor function, to correct distortions automatically, to calculate angles and distances, and to correct easily erroneously digitized coordinates during analysis. Simple animation tools (stick finger function) of the software help to control data of complete sequences, e. g., to identify and correct confusion of left and right limbs. Skeletal landmarks were captured and their x–y coordinates saved for each frame. The coordinates were used to define vectors and to calculate angles between vectors.

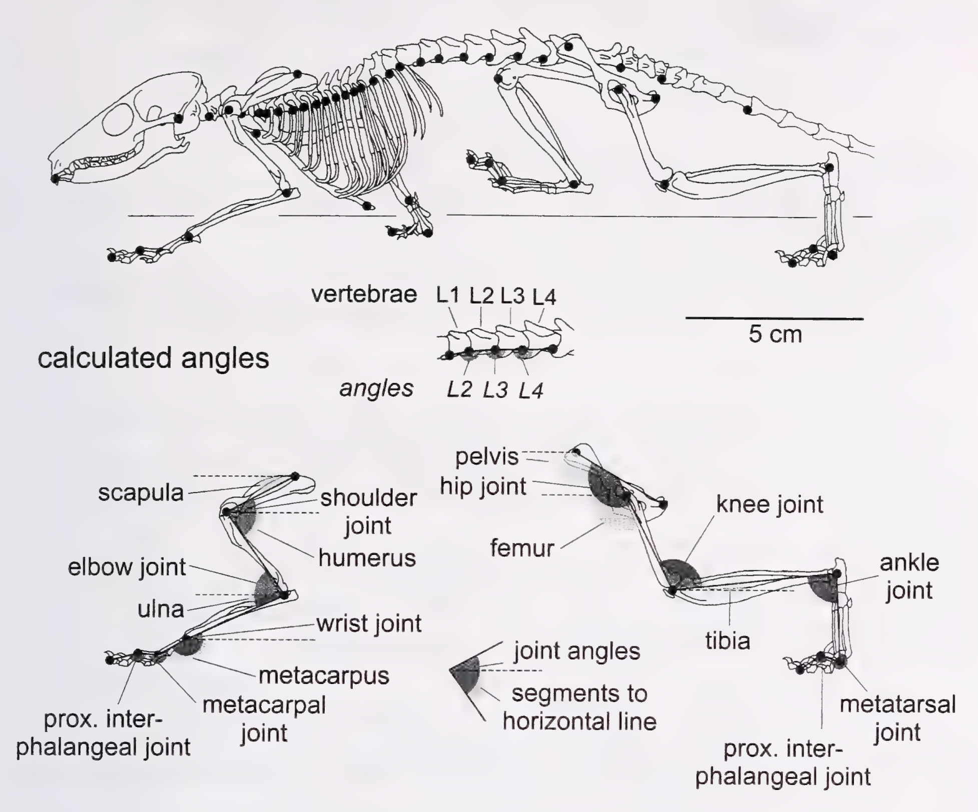


Fig. 1. Skeletal landmarks and calculated angles

Angles were defined anatomically, except for the most proximal ones which were calculated against the horizontal plane. Angle values given in the study represent the projection of the actual angles onto the sagittal plane. The position of digitized landmarks and calculated angles in the parasagittal plane are illustrated in figure 1. Maximum and effective angular movement, timing of segment and limb joint movements and metric gait parameters were analysed. Horizontal and vertical distances, such as the heights of fulcra or step lengths, were measured in cartesian coordinates.

The accuracy of digitization is affected by the contrast of the bones caused by different thickness of proximal and distal body parts. The applied radiation doses were a compromise between the optimal contrast of the proximal and of the distal limb parts. On the same image the most proximal parts are sometimes too dark and the autopodia are too light. The error of landmarks was tested by repeating digitization of five different frames five times. Mean value and standard deviation were calculated for joint angles, segment angles and for x and y coordinates. The average of the standard deviations indicates the digitization error. We estimated digitization errors to be: 1° for elbow, knee and ankle, oints, 2° for shoulder and hip joints, 3° for wrist joint as well as 5° for metacarpo- and metatarso-phalangeal joints. The digitization error for the most proximal elements (scapula, pelvis) is lower than 1°. Because of the high frequent undulation of digitization errors of the intervertebral joint movements, those data were analysed by Fourier transformation.

There are different methods to calculate the contribution of movements of a particular limb segment to stance propulsion. Fischer and Lehmann (1998) proposed a new approach ('overlay method') for calculating the relative contribution of angular movements, to stance propulsion considering the displacement of fulcra of limb segments.

Calculations are based on mean values of typical gait sequences, of which stance and swing phases are set in the same duration using the method of linear interpolation (Fig. 5, 7) (for details see FISCHER and LEHMANN 1998).

Definitions

touch down: hard contact of foot at the beginning of stance.
lift off: last moment of ground contact at the end of stance.
sequence (one step): from the instance of one foot down to the next foot down of the same foot, including one stance and one swing phase.
scene: film section including several successive sequences.
stride length (s [m]): horizontal distance covered by the trunk or a limb during a one step cycle. It consists of stance length and swing length and is calculated for treadmill analyses by:

$$s = \frac{s_{stance}}{t_{stance}} \times t_{swing} + s_{swing}$$

stance length (s_{stance} [m]): horizontal distance between the point of foot down and that of lift off, it corresponds to the amount of trunk propulsion in unrestrained locomotion.
swing length (s_{swing} [m]): horizontal distance between the point of lift off and that of foot down.
stride duration (t [s]): period of time from one foot down event to the subsequent foot down event of the same limb.
stance duration (t_{stance} [s]): time period between foot down and lift off of a limb.
swing duration (t_{swing} [s]): time period between lift off and foot down of a limb.
duty factor (D [%]): ratio of stance time to stride duration.
stride frequency (f [s^{-1}]): 1 / stride duration.
animal's speed: has to be calculated for the case of treadmill running by:

$$v = \frac{s_{stance}}{t_{stance}} + \frac{s_{swing} - s_{stance}}{t_{swing} + t_{swing}}$$

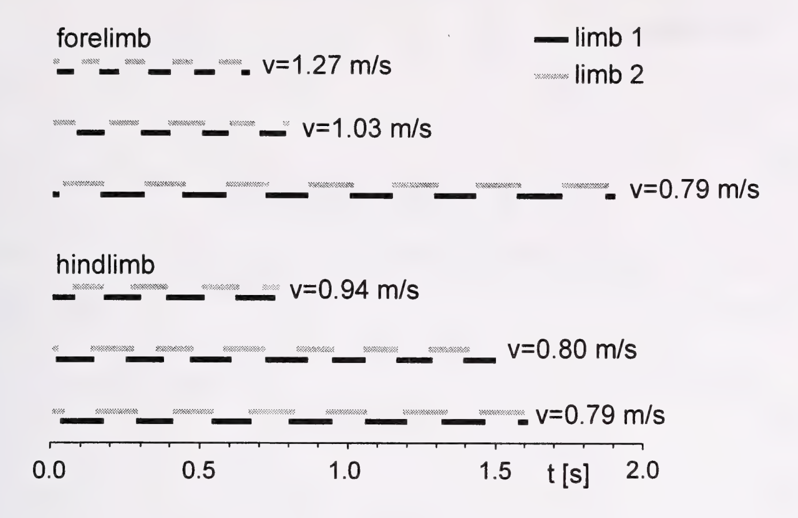
effective angular movement [°]: difference between foot down angle and lift off angle.
maximum angular movement (amplitude) [°]: difference between the maximal and minimal value of angle during the stance or swing phase, respectively.

Results

Metric gait parameters (Tab. 1)

The definition of gaits according to HILDEBRAND (1976, 1977) is based on the behaviour of all four limbs during locomotion. For technical reasons we had to record fore- and hindlimbs separately. Therefore, we distinguish between symmetrical (walk, trot) and in-phase gaits (gallop, bound), the latter are defined by an extensive common ground contact interval and a common suspension period. We could hardly distinguish walk from trot, because transitions occurred from one step to another, so they were both included into the category 'symmetrical' gait. All observed in-phase gaits were gallops. The distal elements of the forelimbs were sometimes out of the X-ray screen and only proximal segments could be analysed. Only 6 complete in-phase steps were available for calculating metric parameters. The gait pattern of the analysed cineradiographic scenes are illustrated in Fig. 2.

Forelimb sequences were registered at velocities between 0.54 m/s–1.56 m/s. Symmetrical gaits and in-phase gaits overlap in a range from 0.97 m/s–1.56 m/s. There is no correlation between gait and speed. Hindlimb sequences were recorded at velocities between 0.71 m/s–2.06 m/s. A gap between symmetrical and in-phase gaits was observed at 1.00 m/s–1.32 m/s. Only one step was filmed in this range, at 1.11 m/s.



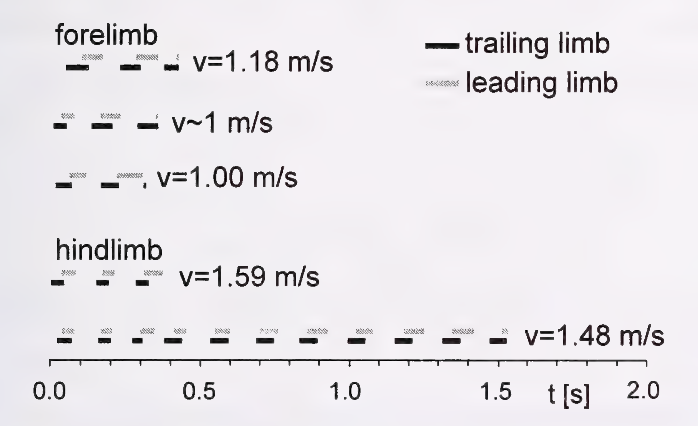


Fig. 2. Footfall pattern of the sequences analysed at different gaits. During in-phase gaits trailing and leading limbs (first and second touching ground) are distinguished.

Stride duration diminishes with increasing speed in symmetrical gaits on fore- and hindlimbs (Fig. 3). Reduction of stride duration is caused by a decrease of stance and swing duration (forelimbs) or stance duration only (hindlimbs). Stance and swing duration were hardly altered at gallop; the resulting stride duration being nearly constant. Speed and stance duration were not correlated on forelimb and on hindlimbs, only swing durations being slightly increased. All duty factors (D) at gallop are less than 50 % on both pairs of limbs. In symmetrical gaits all calculated values account to more than 50 %. With increasing velocity, duty factor decreases.

Forelimb step length slightly decreases with increasing speed at symmetrical gaits caused by decreasing stance and swing lengths (Fig. 4). All limbs travelled longer dis-

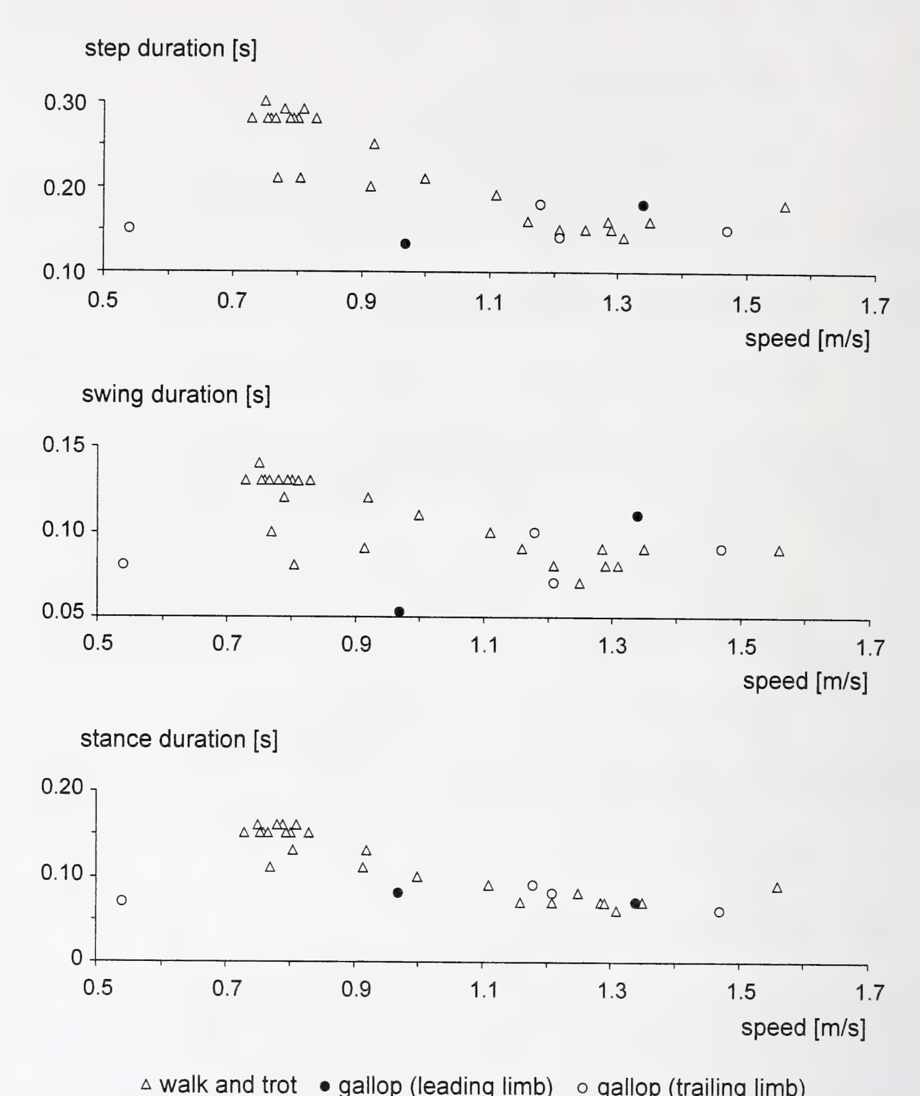


Fig. 3 a. Temporal metric gait parameters a) forelimb, b) hindlimb

tances during swing at symmetrical gaits. At gallop, we found a slight decrease in stance length and increase in swing length at higher speeds. On the hindlimb an increase of step length during all gaits is exclusively accounted for increased swing lengths.

Tupaia gains higher speeds by increasing forelimb step frequency in symmetrical gaits. The insufficient data base for in-phase gaits renders it difficult to decide how higher speeds are attained; most probably by an increase of step length. On the hindlimb the animal takes up speed by an increase of swing length in symmetrical gaits and at gallop by longer steps including a suspension period.

The horizontal distances between scapular fulcrum and finger tips (Tab. 2/a) and Porus acusticus externus and finger tips (Tab. 2/b) were calculated for analysing the re-

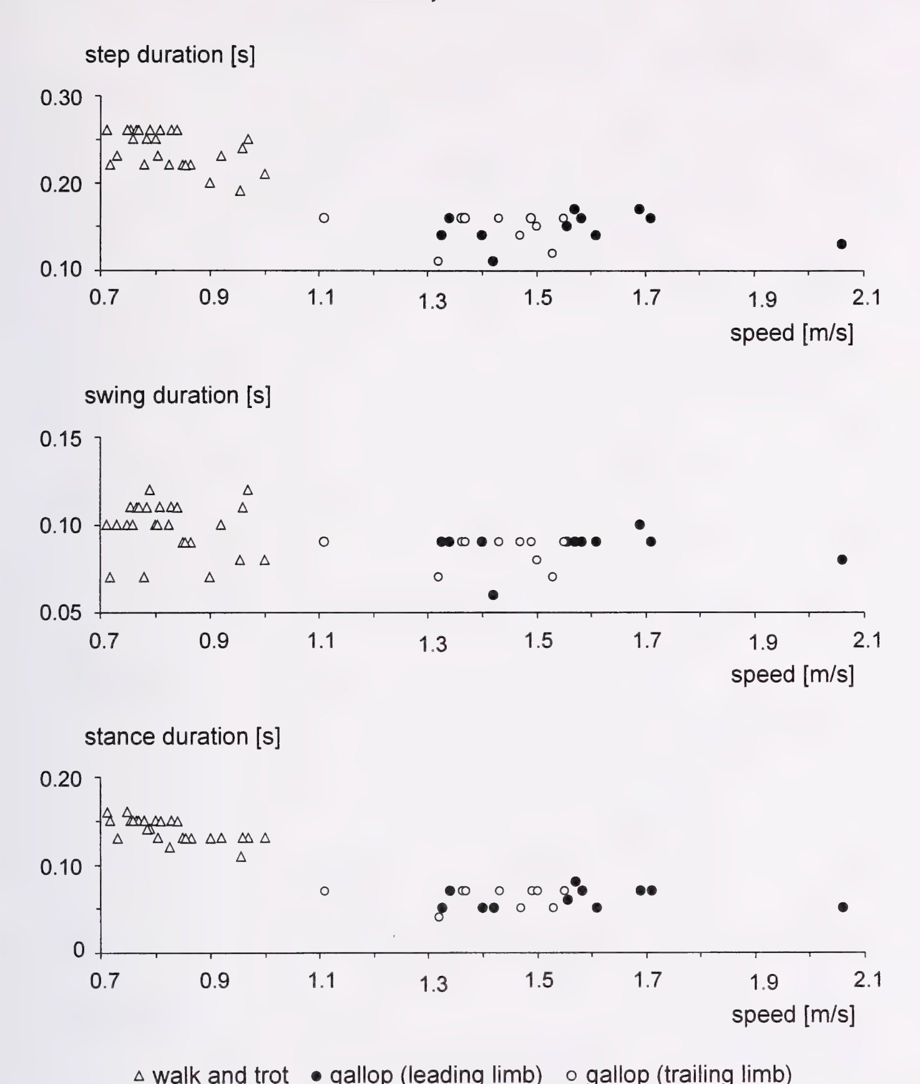


Fig. 3b.

duction of stance length. The latter can be reduced by earlier foot down, lift off or both. The place of foot down is nearly constant at all gaits. Analysed distances between scapular fulcrum and finger tips did not correlate with animal speed or with scapular angle at foot down. However, the extension of the shoulder joint at foot down correlates with this distance during symmetrical gaits. In contrast the shoulder joint is not more extended with greater distances at gallop, but the place of lift off changes with different speeds and gaits. With higher speed, the position of finger tips at lift off is more craniad than at lower speeds. Finally, at gallop the place of lift off lies anterior to the scapular fulcrum. Therefore, stance length is reduced by lift off. The place of foot down is always beneath the eye.

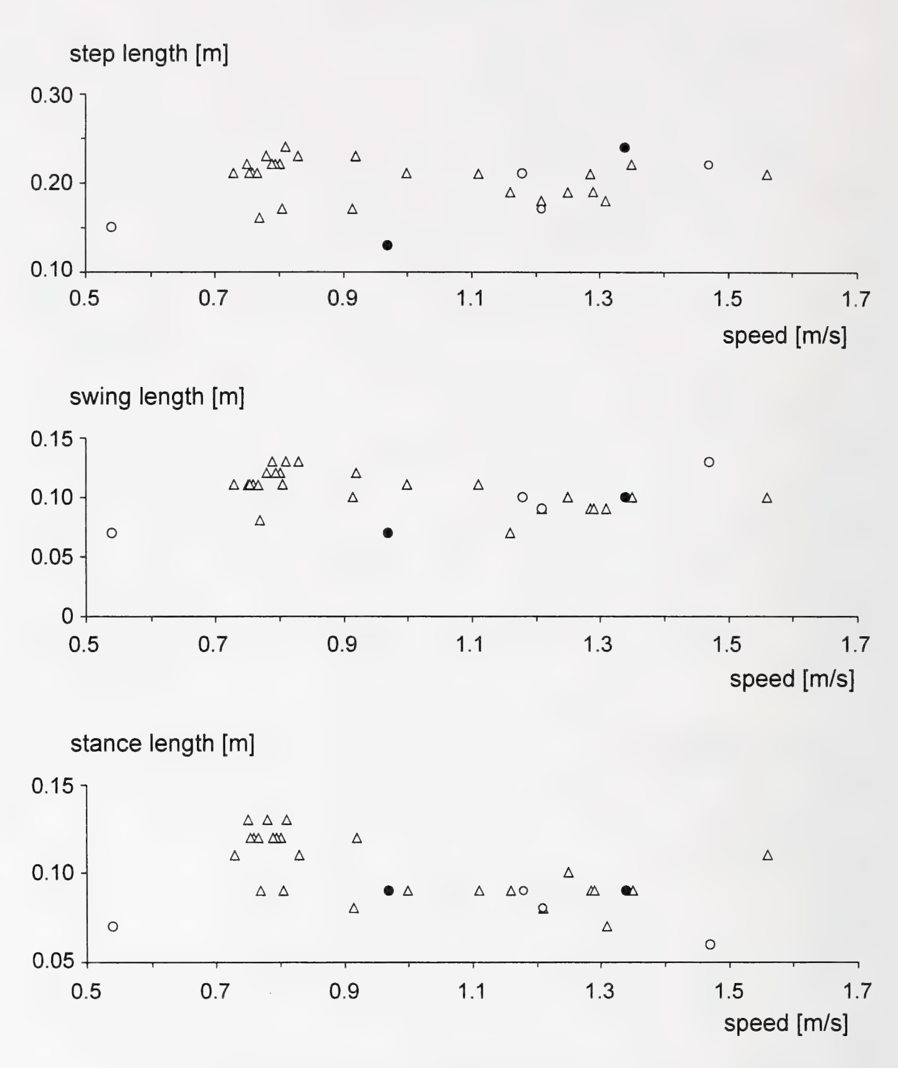


Fig. 4 a. Linear metric gait parameters a) forelimb, b) hindlimb

Kinematics

Forelimb (Fig. 5, Tab. 3)

Scapular movements: The point of intersection of the Spina scapulae and Margo vertebralis is assumed to lie close to the scapular fulcrum. Retroversion of the scapula (syn. caudal rotation in FISCHER 1994, or extension in the sense of MILLER and VAN DER MECHÉ 1975; ENGLISH 1978; BOCZEK-FUNCKE et al. 1996) begins with an angle of the scapular spine to the horizontal line of 38° during symmetrical gaits and 45° at gallop. At lift off, this angle amounts to 92° at a walk and trot or 85° at gallop, but its maximal value (90°–



Fig. 4 b.

95°) is already reached after 85 % of stance duration. Thus, anteversion sets on before foot up. The scapula follows the shape of the thorax during its cranial movement. As the latter becomes narrower anteriorly, the scapula also moves medially. We could not quantify this movement because of the small size of the animal. The onset of retroversion is after 82 % of swing duration during symmetrical gaits or 74 % at gallop. The smaller amplitude and effective angular movement at gallop is caused by lower cranial and caudal movements. Translation of the scapula in horizontal or vertical direction is small and limited by the clavicula and could not be quantified.

Table. 1. Mean values ± standard deviations (first line) and minimum – maximum (second line) of metric gait parameters.

	walk and trot		gallop	
	forelimb	hindlimb	forelimb	hindlimb
N	25	26	6	21
s [m]	0.21 ± 0.02 (0.16 – 0.24)	0.20 ± 0.02 (0.16 – 0.24)	0.19 ± 0.04 (0.13 – 0.24)	0.22 ± 0.04 (0.15 – 0.29)
S_{stance} [m]	0.10 ± 0.02 (0.07 – 0.13)	0.11 ± 0.01 (0.10 – 0.13)	0.08 ± 0.01 (0.06 – 0.09)	0.09 ± 0.02 (0.06 – 0.13)
S_{swing} [m]	0.11 ± 0.02 (0.07 – 0.13)	0.10 ± 0.01 (0.07 – 0.12)	0.09 ± 0.02 (0.07 – 0.13)	0.10 ± 0.03 (0.04 – 0.14)
t [s]	0.23 ± 0.06 (0.14 – 0.30)	0.24 ± 0.02 (0.19 – 0.26)	0.16 ± 0.02 (0.13 – 0.18)	0.15 ± 0.02 (0.11 – 0.17)
t_{stance} [s]	0.12 ± 0.04 (0.06 – 0.16)	0.14 ± 0.01 (0.11 – 0.16)	0.07 ± 0.01 (0.06 – 0.08)	0.06 ± 0.01 (0.04 – 0.08)
t_{swing} [s]	0.11 ± 0.02 (0.07 – 0.14)	0.10 ± 0.01 (0.07 – 0.12)	0.08 ± 0.02 (0.05 – 0.11)	0.09 ± 0.01 (0.07 – 0.10)
D [%]	51 ± 5 (43 – 57)	59 ± 4 (52 – 65)	47 ± 8 (39 – 62)	42 ± 4 (36 – 47)

Table. 2. Mean values ± standard deviations of the distances between a) scapular fulcrum and finger tips and b) Porus acusticus externus and finger tips at foot down and lift off.

			foot down		lift off	
		N	a [mm]	b [mm]	a [mm]	b [mm]
walk and trot	0.79 m/s	13	69 ± 3	24 ± 3	26 ± 5	96 ± 4
	1.03 m/s	7	69 ± 4	24 ± 4	9 ± 4	71 ± 4
	1.27 m/s	8	66 ± 5	21 ± 5	5 ± 5	68 ± 5
gallop	1.00 m/s	4	50 ± 8	4 ± 8	–7 ± 5	56 ± 5
	≈ 1 m/s	4	65 ± 8	17 ± 8	–4 ± 4	59 ± 5
	1.18 m/s	4	72 ± 5	25 ± 25	4 ± 4	66 ± 8

Shoulder joint: Maximal extension in the shoulder joint was observed after 91 % of swing duration during all gaits. The subsequent flexion begins before foot down, when the shoulder joint angle reaches 123° during symmetrical gaits and 131° at gallop. During symmetrical gaits, it lasts 55 % of stance period, then the following extension continues until very late stance. The angle at lift off is 80°. Lift off is initiated by flexion of the shoulder joint which ends after 37 % of the swing phase. The subsequent extension goes on until shortly before foot down. At gallop, we found a major difference in the scheme of shoulder movement. During the whole stance phase the joint is continuously flexed. The maximum angle occurs at its beginning but the minimum angle (56°) is assumed only at 26 % of the swing phase. So, the extension observed in the second half of stance during symmetrical gaits is lacking at gallop.

Humerus: The humerus has an almost vertical position at foot down (85° at symmetrical gaits and 87° at gallop). During symmetrical gaits, the humerus moves during the subsequent retroversion always over and above its horizontal orientation up to a minimal angle (–19°) after 79 % of stance duration. Until lift off, it is lowered by synchronous extensions in the shoulder and elbow joints (–12°), but immediately afterwards the angle

increases to –22°. Humerus anteversion begins on average after 26 % of the swing phase. The retroversion sets on before foot down with a minimum angle of 99°. In contrast to symmetrical gaits, the humerus is retroverted at gallop during the whole stance phase until 11 % of swing duration to up to –17°. The lift off position is at –13°.

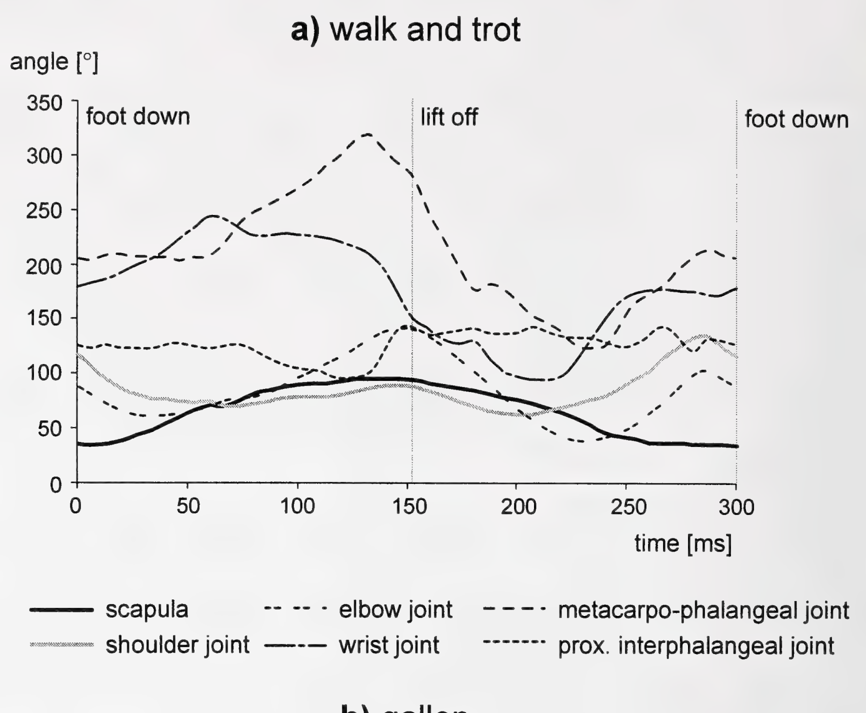
Elbow joint: The elbow joint is flexed starting from a nearly right angle at foot down in the first part of stance (36 % of stance duration at symmetrical gaits, 49 % at gallop). The subsequent extension reaches its maximum (124° at symmetrical gaits, 91° at gallop) at lift off (54 % of steps) or slightly earlier. Flexion reaches its minimum angle of 30°–40° early in swing (38 % of swing duration) at gallop or at midswing (54 %) during symmetrical gaits. The maximum angle (120°–128°) is found shortly before foot down (93 % of swing duration). The elbow joint angle at foot up is 30° greater at gallop than during symmetrical gaits and flexion is stronger at foot down during symmetrical gaits. Effective and maximum angular movements at gallop are smaller than during symmetrical gaits.

Lower arm : The lower arm is orientated horizontally at foot down in 78 % of the observations during all gaits. This minimum angle is achieved after 72 % of swing duration. The averaged angles at foot down are 8° during symmetrical gaits and 18° at gallop. Subsequently, retroversion occurs until the end of the stance phase. Angles at lift off are 138° during walk and trot or 105° at gallop. Maximum and effective angular movement are similar during all gaits.

Hand: The hand is placed in a semidigitigrade position, then lowered so that the whole palm is on the ground during all gaits. At midstance, initiated by palmar flexion in the wrist joint, the hand parts are successively lifted off the ground until finally only the tip of the hand maintains ground contact. In the wrist joint, palmar flexion also begins before foot down after 79 % of swing duration, at an angle of 187° during all gaits. Touch down angles amount to 176° during symmetrical gaits and 183° at gallop. During the first half of the stance phase the wrist joint is dorsally flexed up to a maximum of 238° during symmetrical gaits and 223° at gallop. Palmar flexion begins at midstance. After lift off at an angle of 154° during symmetrical gaits or 149° at gallop, palmar flexion continues steadily into the first third of the swing phase (minimum angle of 98° and 107°). No movements occur in the joint between carpus and metacarpus, therefore we regard both elements acting as one segment (hand) during locomotion. Its angle at touch down is between 11°–18° during all gaits. A minimum angle of –5° is reached after 77 % of the swing phase. The maximum angle of 171° is reached after 10 % of swing duration. Maximum angle and angle at lift off (270°–290°) in the metacarpo-phalangeal joint were identical in 97 % during all gaits. Minimal angle occurs during swing (109°–134°) after 46 % of swing duration at all gaits. Angles at foot down are 206°–222°. Values of the proximal interphalangeal joint scatter largely and are not presented in the tables. During the stance phase, only minor movements are observed. The angle at foot down is about 115° and about 140° at lift off in more than half of the values.

Hindlimb (Fig. 7, Tab. 4): On the hindlimb we distinguish trailing and leading limbs during in-phase gaits. Despite our relatively small sample, we were able to characterize different limb behaviours. The difference at foot down and lift off between both limbs is up to 28 ms (N = 21) at an averaged step duration of 150 ms.

Spine movements (Fig. 6): Any small additive vertebral spine movements will result in a displacement of the pelvis because of its immobility in the iliosacral joint. Despite this fact, we call the coupled displacements of pelvis ‘pelvic movement’ for the sake of simplicity. The angle between pelvis and sacral vertebrae remains constant at 21° during locomotion. During symmetrical gaits, angles in the intervertebral joints from Th3 to L5 are between 170° and 180° (N = 5) (Fig. 6) during step. Consequently, ‘pelvic movements’ are only very small; the difference between the angle at foot down and lift off is only 4°. But at walk and trot two additional ‘pelvic movements’ were observed. First, a rotation about the dorsoventral axis is discernible, caused by the lateral additive intervertebral joint



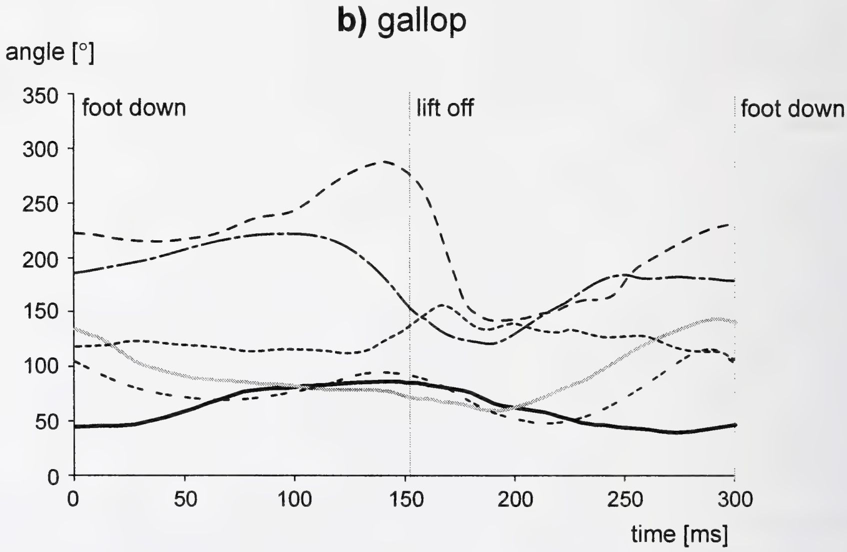


Fig. 5. Scheme of angular movements of forelimb joints a) during symmetrical gaits and b) at gallop

Table. 3. Mean values ± standard deviations of angles at foot down, lift off, minima and maxima in the stance and swing phase of the forelimb (if standard deviation is missing only one value was available).

		walk and trot			gallop		
forelimb	v [m/s]	0.79	1.03	1.27	≈ 1	1.00	1.18
	N	13	7	8	4	4	4
scapula	down	35 ± 3	41 ± 4	39 ± 6	41 ± 5	46 ± 2	48 ± 9
	lift off	95 ± 5	89 ± 5	90 ± 6	86 ± 10	86 ± 1	84 ± 14
stance	min	34 ± 3	39 ± 4	38 ± 5	39 ± 5	43 ± 6	93 ± 11
	max	97 ± 5	94 ± 2	94 ± 4	90 ± 6	88 ± 2	48 ± 9
swing	min	32 ± 3	39 ± 3	36 ± 4	34 ± 6	37 ± 6	39 ± 5
	max	95 ± 5	92 ± 3	90 ± 6	81 ± 6	85 ± 4	82 ± 15
shoulder joint	down	124 ± 7	125 ± 13	120 ± 12	118 ± 12	140 ± 9	136 ± 13
	lift off	89 ± 6	74 ± 8	72 ± 11	67 ± 7	76 ± 5	73 ± 8
stance	min	67 ± 4	56 ± 5	60 ± 12	67 ± 7	74 ± 3	73 ± 8
	max	124 ± 7	122 ± 15	120 ± 12	118 ± 12	140 ± 9	136 ± 13
swing	min	59 ± 2	56 ± 6	48 ± 6	58 ± 4	53 ± 13	57 ± 7
	max	138 ± 6	14 ± 26	134 ± 10	150 ± 6	149 ± 17	144 ± 15
humerus	down	89 ± 7	83 ± 10	81 ± 12	77 ± 17	93 ± 9	88 ± 13
	lift off	–6 ± 3	–15 ± 4	–18 ± 7	–19 ± 10	–10 ± 6	–11 ± 6
stance	min	–16 ± 3	–19 ± 4	–23 ± 4	–19 ± 10	–10 ± 5	–13 ± 4
	max	89 ± 7	83 ± 10	84 ± 14	77 ± 17	93 ± 9	88 ± 13
swing	min	–18 ± 3	–23 ± 1	–28 ± 3	–23 ± 6	–14 ± 11	–15 ± 7
	max	102 ± 6	100 ± 5	95 ± 8	110 ± 2	104 ± 16	99 ± 8
elbow joint	down	89 ± 9	92 ± 10	90 ± 12	95 ± 14	113 ± 13	109 ± 11
	lift off	139 ± 10	116 ± 10	108 ± 23	83 ± 20	93 ± 5	98 ± 12
stance	min	60 ± 3	58 ± 5	59 ± 4	62 ± 9	72 ± 4	72 ± 3
	max	144 ± 5	118 ± 9	113 ± 22	102 ± 11	114 ± 11	113 ± 8
swing	min	36 ± 4	27 ± 5	31 ± 3	40 ± 4	47 ± 14	42 ± 10
	max	141 ± 8	119 ± 6	117 ± 16	123 ± 9	123 ± 24	114 ± 12
lower arm	down	6 ± 4	9 ± 3	9 ± 6	18 ± 8	20 ± 7	21 ± 4
	lift off	150 ± 4	131 ± 7	126 ± 17	101 ± 12	103 ± 6	110 ± 16
stance	min	6 ± 4	9 ± 3	9 ± 6	17 ± 8	20 ± 7	20 ± 5
	max	151 ± 4	133 ± 8	129 ± 16	103 ± 11	103 ± 6	113 ± 12
swing	min	–3 ± 4	–3 ± 3	–4 ± 3	–6 ± 5	4 ± 4	2 ± 2
	max	150 ± 4	133 ± 6	124 ± 17	101 ± 12	104 ± 7	110 ± 16
wrist joint	down	178 ± 4	172 ± 6	176 ± 5	188 ± 2	188 ± 9	184 ± 3
	lift off	146 ± 30	158 ± 14	164 ± 22	153 ± 14	157 ± 15	137 ± 18
stance	min	143 ± 29	157 ± 14	162 ± 18	226 ± 5	163 ± 10	137 ± 18
	max	248 ± 5	227 ± 12	233 ± 5	153 ± 14	222 ± 3	223 ± 3
swing	min	85 ± 7	107 ± 15	111 ± 9	95	114 ± 7	111 ± 7
	max	183 ± 3	191 ± 6	191 ± 5	184	191 ± 1	188 ± 3
carpus+	down	11 ± 3	18 ± 3	14 ± 3	15 ± 1	15 ± 6	17 ± 3
metacarpus	lift off	170 ± 17	153 ± 12	141 ± 14	128 ± 4	126 ± 12	152 ± 5
stance	min	1 ± 4	7 ± 2	7 ± 7	1 ± 1	12 ± 2	10 ± 3
	max	170 ± 17	153 ± 12	141 ± 14	128 ± 4	126 ± 12	152 ± 5
swing	min	0 ± 3	–9 ± 8	–8 ± 4	–	–6 ± 7	–1 ± 3
	max	197 ± 7	172 ± 6	178 ± 13	–	149 ± 18	161 ± 8
metacarpo-	down	206 ± 10	222 ± 4	219 ± 10	221 ± 2	220 ± 16	222 ± 9
phalangeal j.	lift off	280 ± 24	286 ± 15	289 ± 11	281 ± 21	277 ± 11	273 ± 13
stance	min	196 ± 6	210 ± 4	210 ± 5	208 ± 6	212 ± 3	211 ± 5
	max	326 ± 6	304 ± 9	293 ± 6	289 ± 1	284 ± 9	298 ± 17
swing	min	109 ± 9	124 ± 9	134 ± 16	112	132	132 ± 15
	max	280 ± 25	289 ± 14	288 ± 11	241	244	233 ± 25

movements ('lateral bending', Jenkins and Camazine 1977). It was estimated using the horizontal distance (x-coordinates) between hip joints in lateral projection. This horizontal distance between hip joints reaches an averaged maximum of 3 mm when foot down

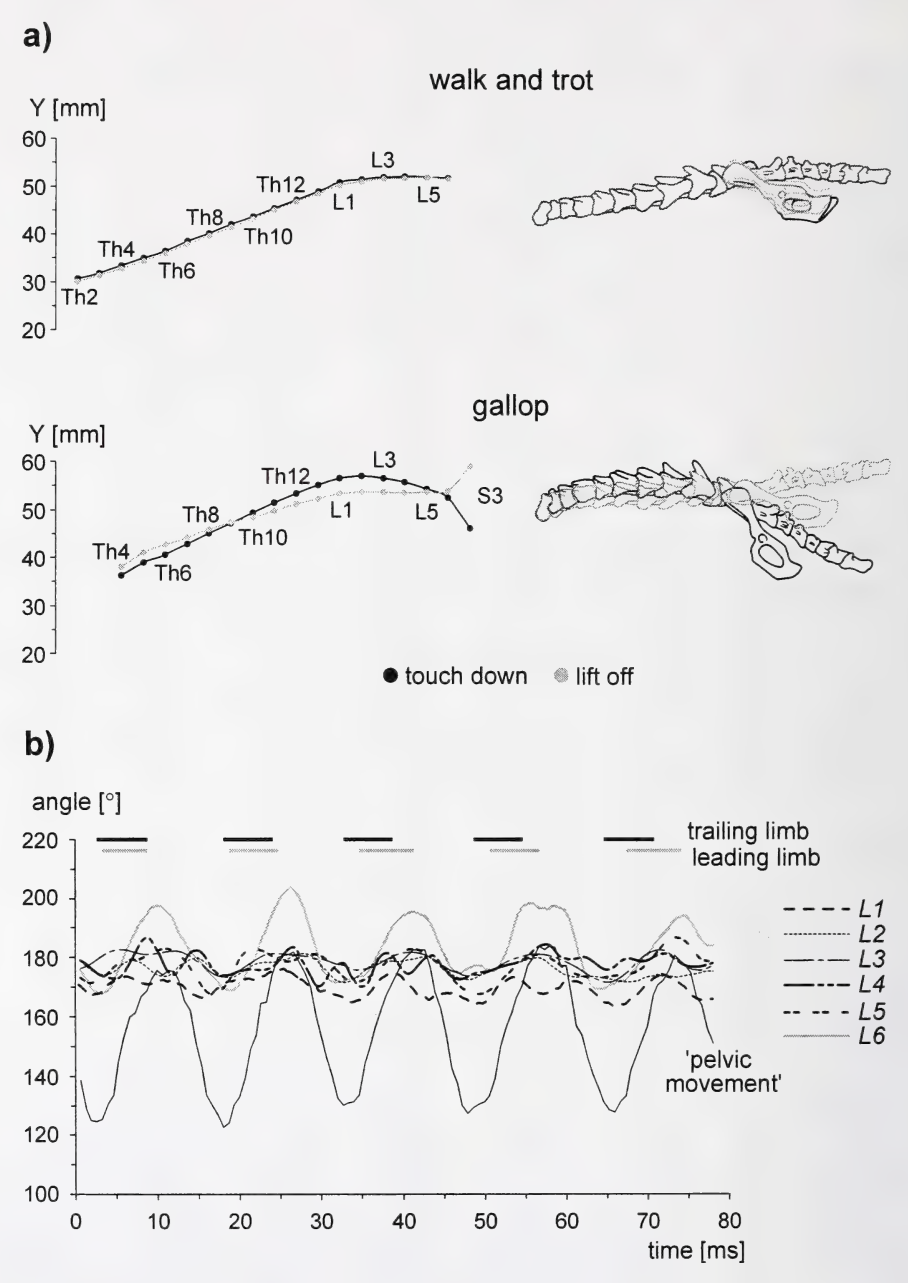


Fig. 6. Sagittal spine movements, a) height of vertebrae over the ground during symmetrical gaits and at gallop; additive sagittal spine movements and resulting 'pelvic movement' at foot down and lift off (for the left foot during symmetrical gaits and for the trailing limb at gallop); b) amplitudes of intervertebral lumbar spine bendings and resulting 'pelvic movements'

takes place on one limb and foot up on the other limb. It corresponds to an angle of approximately 8° of rotation about the dorsoventral axis, with a range of 5–13° during all sequences. The second 'pelvic movement' is a rotation about the longitudinal axis ('tilting', JENKINS and CAMAZINE 1977). It was calculated from the vertical distance (y-coordinates) between both hip joints with up to 5°. At gallop, extensive sagittal 'pelvic movements' occur. Pelvic retroversion begins after 91 % (trailing limb) or 79 % of leading limb swing duration. It continues into early swing phase before anteversion sets on at 22 % of trailing or leading limbs swing phase. Different individuals seem to have different amplitudes at similar speeds (39° at v = 1.48 m/s, 28° at v = 1.59 m/s) resulting from different angles at foot down (Tab. 4). The cranial angle between the longitudinal axis of the pelvis and the horizontal line (Fig. 1) is up to 12° less in the trailing limb than in the leading limb at foot down. At foot up this difference is 7°–13°. Maximum amplitudes of trailing and leading limbs are similar at different speeds. Sagittal spine movements are localised in the posterior thoracic and lumbar spine (Th11-L6). The angles for the lumbar intervertebral joints are illustrated in figure 6. Intervertebral movements increase caudad: L1–L4: 8°–9°, L5: 13°, L6: 26°. The total excursion of the pelvis is less than the sum of the angles of the single intervertebral joints because the respective angular maximum is achieved successively (43°, N = 5). The propagation wave of the extension starts in the thoracic region and runs caudally. Vertebral flexions begin in the caudal thoracic region followed by the lumbar region. The maximum extension in all vertebral joints is found at lift off or shortly thereafter. Anteversion also starts with flexion in the caudal thoracic intervertebral joints.

Hip joint: Hip, knee and ankle joint kinematics are strikingly different during symmetrical gaits and gallop, the amplitude generally being lower at gallop. The amplitude of the hip joint angle during walk and trot is 110°, but at gallop it is less than 70° (Tab. 4). As step length is more or less the same, the reduced angular movements have to be compensated 'pelvic movements'. The higher amplitude during symmetrical gaits is caused by a stronger extension at lift off (141°, as compared to 110° in trailing and 106° in leading limb), and a stronger flexion at foot down (35° at walk and trot, 38° in leading limb and 110° in trailing limb). The hip joint is continuously extended during stance. Flexion of hip joint lasts for more than 80 % of swing duration, reaching minimum angles of 28° (walk and trot) or 32° (gallop). The angles at foot down in the trailing limb are greater than in the leading limb. Effective angular movements at gallop are half of the movements that may be observed during symmetrical gaits.

Femur: Hip joint movements, and in the case of gallop also sagittal 'pelvic movements', lead to gait-dependent rotations of the femur. Femur retroversion begins after 90 % of swing duration in symmetrical gaits with a minimal angle of 9° below the horizontal line and reaches an angle of 16° at foot down. At gallop (v = 1.48 m/s), the timing of the retroversion is similar but the trailing limb femur is kept almost horizontally and one of the leading limbs is even up to 14° above the horizontal line. In the other gallop scene (v = 1.59 m/s) both femora do not reach a horizontal position, because the pelvis is less anteriorly displaced (see above). Retroversion ends shortly before or at lift off. Averaged angles at lift off are about 20° higher during symmetrical gaits than at gallop. In the latter, retroversion of the segment continues mostly into early swing phase (about 12 % of swing duration).

Knee joint: The amplitude in the knee joint is 72° during symmetrical gaits but only 48° at gallop. While foot down angles are quite similar (Tab. 4), angles at lift off are markedly (by about 30°) smaller at gallop than during symmetrical gaits (124°). Minimal angles (55°) were noticed after the first part of stance during all gaits, when the ankle joint passes beneath the hip joint. Flexion lasts up to 43 % of the trailing limb's stance duration or 40 % of stance phase of the leading limb and for 27 % of the stance phase during symmetrical gaits. During symmetrical gaits, extension is finished in 30 % of steps at lift

off, in 10 % one frame (1/150 s) later and in 60 % one frame earlier. At gallop, it coincides with lift off. After 62 % of swing phase a minimal angle of 42° is observed during symmetrical gaits. It is followed by a brief extension until, finally, flexion begins before foot down. Minimal angles (30°–40°) occur at midstance at gallop.

Tibia /Fibula: The angle of the longitudinal axis of the shank to the horizontal line is 49° at foot down during symmetrical gaits. The lower leg is then retroverted to a minimum angle of –11° after 63 % of stance phase. Until lift off it returns to a horizontal position (–1°). A minimal angle of –18° after 36 % of swing duration is notized. Anteversion is terminated shortly before foot down (60° after 89 % of swing duration). At gallop, minimum angles are found after 82 % of stance duration in the trailing limb and 76 % in the leading limb. Angles at lift off are smaller in the trailing limb than in the leading limb. Retroversion begins always before foot down in both limbs after 87–88 % of swing duration. The shank is never found in a vertical but always in caudal orientations.

Ankle joint (talocrural joint): Maximum amplitude at gallop is about 30° lower than that at walk or trot (Tab. 4), although angles at foot down are larger (71° as compared to 58°) during symmetrical gaits. At lift off the ankle joint is > 35° more extended during symmetrical gaits than at gallop. Initial dorsal flexion is observed at 17 % of the stance phase during these gaits, but significantly later in the trailing limb (38 %) or leading limb (40 %). The succeeding plantar flexion ends slightly before lift off (14 % of steps), at lift off (38 %), or, in 48 % of observations, after 8 % of the swing phase at walk and trot. Plantar flexion of the trailing limb lasts in all sequences into the swing phase, that of the leading limb only in two thirds of steps. In the other cases, plantar flexion of the leading limb ends at lift off. The subsequent dorsal flexion continues for two thirds of the swing phase during all gaits. After a short plantar flexion the dorsal flexion begins, which lasts until stance phase.

Foot: Six steps were analysed to estimate movements between tarsus and metatarsus. Movements in the tarso-metatarsal joint are found at foot down and immediately afterwards with a dorsal flexion of about 15°. During the remainder of the step we observed an angle of nearly 180° in this joint. Therefore, tarsus and metatarsus were regarded as one segment. Its retroversion begins always just before foot down during walk and trot. After foot down (9°), the retroversion lasts until the end of stance (34 % of steps) or into the swing phase (66 % of observations). Angles at lift off reach 138°. Angles at lift off were smaller at gallop than at walk or trot as a consequence of smaller angles in the talocrural joint. Anteversion ends considerably later than dorsal flexion in the ankle joint at about 85 % of swing.

Metatarso-phalangeal joint: After foot down at an angle of 217°, the joint is dorsally flexed to a maximum of 312° after 74 % of stance duration during symmetrical gaits. Angles at lift off are widely scattered; the averaged angle is 250°. Plantar flexion during swing phase reaches a minimum angle of 156° after one-third of swing duration in 34 % of the steps, or after two-thirds of swing in 66 % of the steps. The subsequent dorsal flexion continues into the stance phase. Joint angles and timing at walk and trot are comparable with those at gallop. In the latter, minimum angles occur earlier (trailing limb after 38 %, and leading limb after 26 % of swing) during the swing phase, and maximum and effective angular movements are smaller. As in the forelimb, the angles of the proximal interphalangeal joint are scattered and not presented in a table. For example, the maximum angle during stance phase is observed in 40 % of observations (N = 26) in the first half, in 20 % in the second half of stance, and in 40 % at lift off. The angle at foot down is approximately 110° at walk or trot and about 130° at lift off. The maximum angle is after lift off (average 173°). The leading limb has greater effective angular movements and amplitudes than the trailing limb. Angles of the metatarso-phalangeal joint at foot down and lift off are smaller at gallop than at walk and trot (trailing limb: foot down 110°, lift off 112°; leading limb: foot down 105°, lift off: 112°).

Intralimb coordination (Fig. 8): Foot down is initiated by palmar flexion of the wrist, followed by scapula retroversion. Just after 90 % of swing duration synchronous flexions in shoulder and elbow joint begin. Coincident with foot down, dorsal flexion during the stance phase starts in the wrist joint. In the first third of stance extension of the elbow joint and at midstance of the shoulder joint follows. Lift off is introduced by wrist joint

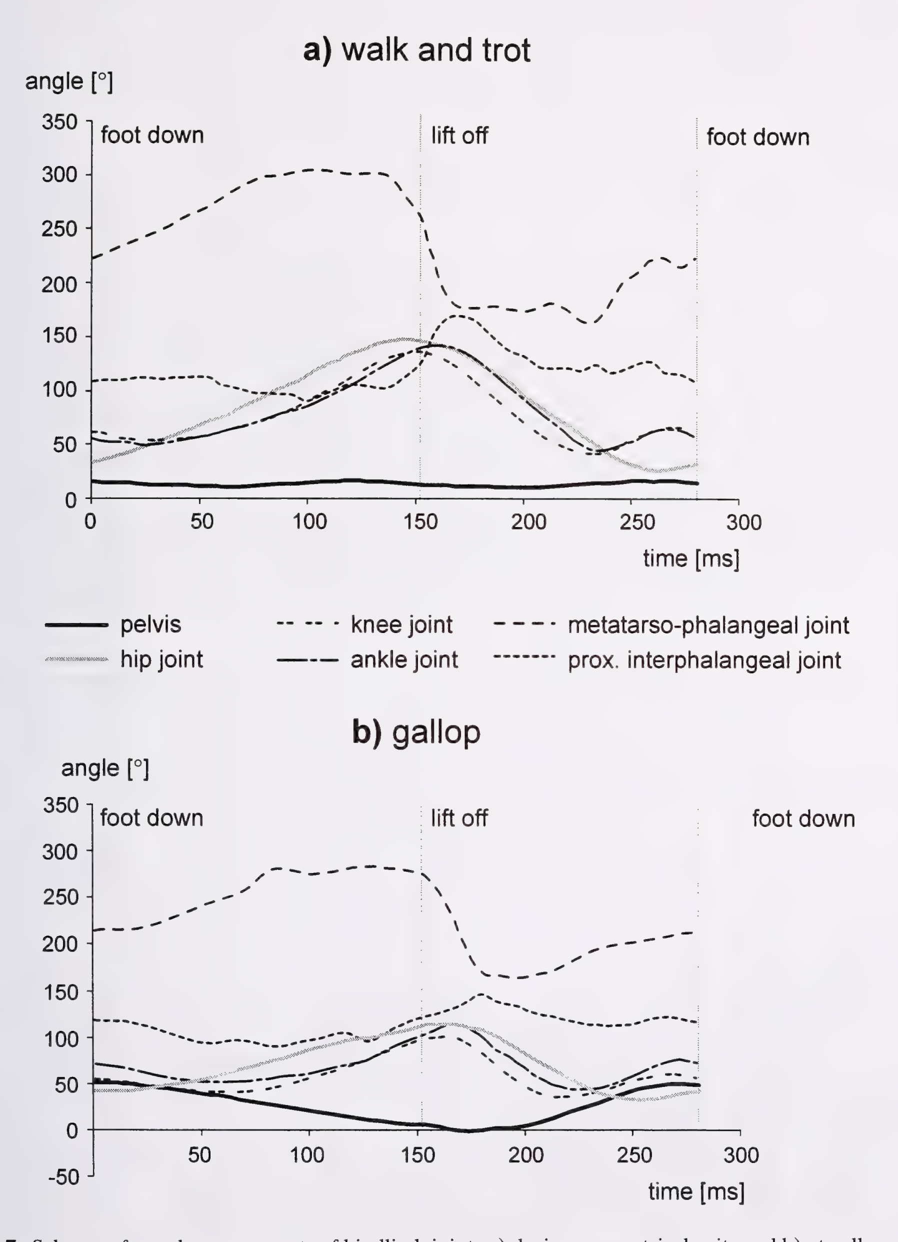


Fig. 7. Scheme of angular movements of hindlimb joints a) during symmetrical gaits and b) at gallop

Table. 4. Mean values ± standard deviations of angles at foot down, lift off, minima and maxima in the stance and swing phase of the hindlimb (if standard deviation is missing only one value was available).

hindlimb		walk and trot			gallop			
	v [m/s]	0.79	0.80	0.94	1.48		1.59	
	N	11	10	5	9 trailing	9 leading	1 trailing	2 leading
pelvis	down	164 ± 4	159 ± 7	159 ± 2	132 ± 7	137 ± 8	143	154 ± 6
	lift off	167 ± 4	163 ± 6	163 ± 5	170 ± 5	177 ± 5	169	182 ± 4
stance	min	161 ± 3	153 ± 4	157 ± 1	131 ± 6	137 ± 8	143	154 ± 6
	max	171 ± 3	169 ± 4	166 ± 4	170 ± 5	178 ± 5	169	182 ± 5
swing	min	161 ± 3	154 ± 4	157 ± 2	131 ± 7	130 ± 6	143	143
	max	171 ± 3	168 ± 6	164 ± 4	182 ± 3	182 ± 4	182	182
hip joint	down	34 ± 4	34 ± 5	42 ± 5	49 ± 6	39 ± 5	55	37 ± 4
	lift off	145 ± 5	135 ± 8	143 ± 10	113 ± 13	112 ± 8	106	100 ± 18
stance	min	33 ± 4	33 ± 5	42 ± 5	48 ± 6	39 ± 5	55	37 ± 5
	max	149 ± 4	139 ± 8	147 ± 7	113 ± 13	112 ± 8	106	100 ± 18
swing	min	25 ± 3	28 ± 4	35 ± 3	32 ± 5	33 ± 3	29	33
	max	146 ± 5	135 ± 8	145 ± 9	115 ± 14	118 ± 8	115	101
femur	down	17 ± 5	13 ± 7	21 ± 5	1 ± 10	–4 ± 11	18	11 ± 6
	lift off	132 ± 7	118 ± 9	126 ± 9	103 ± 16	109 ± 10	95	108 ± 22
stance	min	17 ± 5	13 ± 7	21 ± 5	11 ± 0	–4 ± 11	18	11 ± 6
	max	134 ± 5	120 ± 6	128 ± 6	103 ± 16	109 ± 10	95	108 ± 22
swing	min	9 ± 3	6 ± 4	14 ± 4	–6 ± 10	–14 ± 7	5	4 ± 1
	max	132 ± 7	118 ± 9	126 ± 10	111 ± 14	116 ± 9	109	113 ± 14
knee joint	down	62 ± 4	64 ± 4	70 ± 6	58 ± 7	74 ± 33	71	75 ± 11
	lift off	133 ± 11	112 ± 13	127 ± 14	91 ± 15	87 ± 20	88	108 ± 24
stance	min	54 ± 5	54 ± 7	58 ± 4	45 ± 9	45 ± 11	55	60 ± 11
	max	136 ± 9	115 ± 10	130 ± 12	92 ± 13	104 ± 15	90	110 ± 21
swing	min	42 ± 6	39 ± 5	47 ± 7	37 ± 4	32 ± 3	41	41 ± 9
	max	133 ± 12	112 ± 13	129 ± 15	98 ± 14	112 ± 13	105	110 ± 27
shank	down	45 ± 7	52 ± 5	49 ± 7	57 ± 8	61 ± 11	55	64 ± 12
	lift off	1 ± 5	–5 ± 6	1 ± 7	–12 ± 6	–5 ± 7	–6	0 ± 9
stance	min	–11 ± 4	–12 ± 6	–7 ± 3	–15 ± 7	–10 ± 7	–6	–6 ± 12
	max	45 ± 7	52 ± 5	49 ± 7	57 ± 8	61 ± 11	55	64 ± 12
swing	min	–16 ± 3	–21 ± 8	–14 ± 5	–33 ± 5	–28 ± 7	–39	–29 ± 9
	max	56 ± 4	64 ± 6	61 ± 3	71 ± 7	75 ± 7	68	81 ± 7
ankle joint	down	56 ± 6	57 ± 6	61 ± 7	68 ± 5	71 ± 10	73	73 ± 12
	lift off	139 ± 9	132 ± 13	140 ± 7	95 ± 14	110 ± 21	100	108 ± 28
stance	min	49 ± 5	48 ± 4	54 ± 6	54 ± 6	55 ± 9	65	59 ± 4
	max	140 ± 8	130 ± 14	141 ± 6	96 ± 11	110 ± 21	100	110 ± 25
swing	min	42 ± 6	42 ± 7	49 ± 4	38 ± 4	45 ± 5	49	48 ± 18
	max	142 ± 7	134 ± 13	141 ± 7	110 ± 18	128 ± 16	107	116 ± 28
tarsus+	down	12 ± 3	5 ± 3	12 ± 2	11 ± 4	10 ± 6	18	9 ± 8
metatarsu	lift off	138 ± 6	138 ± 8	138 ± 4	108 ± 17	116 ± 16	99	109 ± 24
stance	min	12 ± 3	5 ± 3	12 ± 2	11 ± 5	11 ± 6	17	9 ± 8
	max	138 ± 6	138 ± 8	139 ± 4	108 ± 17	116 ± 16	99	109 ± 24
swing	min	6 ± 3	1 ± 3	9 ± 3	–5 ± 5	–8 ± 6	10	–4 ± 9
	max	143 ± 5	141 ± 8	140 ± 5	125 ± 16	134 ± 12	133	121 ± 7
metatarso	down	223 ± 10	214 ± 5	212 ± 5	223 ± 9	220 ± 10	227	202 ± 20
phalang. j.	lift off	262 ± 25	270 ± 9	219 ± 30	275 ± 12	273 ± 7	306	243 ± 20
stance	min	220 ± 2	209 ± 15	203 ± 14	219 ± 11	218 ± 13	227	202 ± 19
	max	311 ± 7	312 ± 3	317 ± 5	285 ± 9	289 ± 7	306	279 ± 3
swing	min	155 ± 10	158 ± 11	156 ± 10	154 ± 11	156 ± 7	161	152 ± 6
	max	262 ± 22	276 ± 17	236 ± 17	277 ± 11	272 ± 7	306	221 ± 2

palmar flexion starting already at midstance, followed by scapula anteversion. Flexion in the shoulder and elbow joints coincide with lift off. Extension of the shoulder, elbow and wrist joints begin in the second third of swing phase. Only the shoulder joint shows a strikingly different pattern with gait change. While two flexions and extensions per step were determined during symmetrical gaits, we observed only one flexion and extension per step at gallop. Monophasic extension in the hip joint, flexion of the knee and ankle joints are synchronous and immediately preceding foot down during symmetrical gaits. Additionally, sagittal extensions of the vertebral spine occur at gallop shortly before foot down. Extensions in the knee and ankle joints begin in the first third of stance. Lift off is initiated by a monophasic flexion in the metatarso-phalangeal joint, followed by flexions of the hip and knee joints. The ankle joint flexes dorsally only after lift off. At gallop, the actions of the hip and knee joints are delayed, and start simultaneously with those of the ankle joint after foot up. The onset of anteversion of the pelvis is in the first third of swing phase. The extension in the metatarso-phalangeal joint precedes that of the knee, ankle, and hip joints. With change from walk and trot to gallop shorter flexions in hip and knee joints can be observed.

Body propulsion: The contribution of a limb segment to body propulsion depends on the height of its fulcrum and its effective angular movements. Therefore, the scapula is the main propulsive element in the forelimb during all gaits (42–43 %). For the humerus and the ulna a difference between symmetrical and in-phase gaits occurs. While the humerus contributes only up to 17 % of stance length, it contributes up to 45 % to propulsion at gallop. In contrast, the ulna contributes to propulsion only 3 % at gallop and 32 % at walk and trot. The hand adds 9–10 % of propulsion during all gaits. The contribution of the additive sagittal spine movements to the body propulsion are different between symmetrical and in-phase gaits. At gallop, it amounts to 42 % but at walk and trot only 2 %. Femoral movements account 49 % for propulsion at gallop and 82 % during symmetrical gaits. During all gaits, the shank caused a loss of propulsion (symmetrical gaits: –21 %, gallop: –11 %). The contribution of the whole foot was calculated to be 36 % during symmetrical gaits and 21 % at gallop.

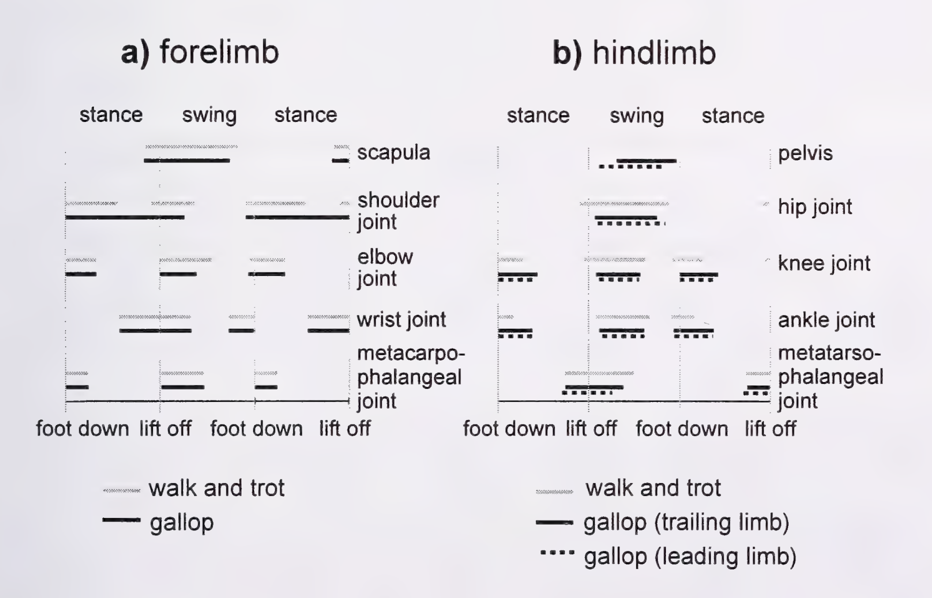


Fig. 8. Intralimb coordination of a) forelimb and b) hindlimb

Heights of the fulcra (Tab. 5): During symmetrical gaits, the most proximal fulcrum on the forelimb (scapular fulcrum) is lower than the hip joint. At gallop, both fulcra are higher than at walk and trot. The scapular fulcrum is situated 43 mm above the ground during symmetrical gaits or 49 mm at gallop: At foot down, the shoulder joint is 32 mm above ground (walk and trot), or 36 mm (gallop). It is lowered down until lift off by 11 mm during symmetrical gaits and 4 mm at gallop. Vertical movement of the elbow joint is higher at gallop (22 mm) than at symmetrical gaits (11 mm). Within a gait, no correlation between those heights and speed are found on the forelimb, whereas on the hindlimb, during symmetrical gaits, the height of the pelvis increases with higher speeds (by 2 mm–4 mm). During symmetrical gaits, constant vertical distances of pelvic and hip joint landmarks above the ground are observed. At gallop, the positions of these points change as a consequence of sagittal spine movements. They are lowered at foot down and rise at lift off. At lift off during walk and trot, the height of the knee joint increases with higher speeds (up to 6 mm) as a consequence of greater extension in the joint.

Table. 5. Heights of fulcra of fore- and hindlimb [mm].

forelimb		walk and trot			gallop		
v [m/s]		0.79	1.03	1.27	1.00	≈ 1	1.18
N		14	8	9	5	6	6
scapular spine	foot down	44 ± 2	41 ± 3	43 ± 2	51 ± 5	47 ± 4	49 ± 5
	lift off	41 ± 2	41 ± 3	44 ± 2	51 ± 3	48 ± 6	49 ± 5
shoulder joint	foot down	33 ± 1	29 ± 1	31 ± 1	37 ± 5	35 ± 4	37 ± 4
	lift off	18 ± 2	25 ± 3	23 ± 3	33 ± 4	30 ± 4	32 ± 5
elbow joint	foot down	6 ± 1	7 ± 2	6 ± 2	12 ± 3	11 ± 2	12 ± 2
	lift off	22 ± 1	31 ± 3	31 ± 5	38 ± 1	38 ± 3	36 ± 2
wrist joint	foot down	2 ± 0	4 ± 0	3 ± 0	4 ± 1	5 ± 2	4 ± 1
	lift off	8 ± 2	11 ± 1	12 ± 1	12 ± 2	13 ± 2	13 ± 1
metacarpo-	foot down	1 ± 0	2 ± 0	2 ± 0	2 ± 1	1 ± 0	2 ± 0
phalangeal joint	lift off	8 ± 2	7 ± 1	6 ± 2	5 ± 2	6 ± 2	8 ± 1
proximal	foot down	2 ± 1	3 ± 0	4 ± 0	3 ± 1	3 ± 0	4 ± 0
interphalangeal joint	lift off	4 ± 1	4 ± 1	4 ± 1	3 ± 1	4 ± 1	4 ± 1

hindlimb		walk and trot			gallop	
v [m/s]		0.8	0.8	0.97	1.48	1.59
N		13	13	7	22	6
Tuber coxae	foot down	53 ± 2	52 ± 1	57 ± 3	57 ± 5	58 ± 3
	lift off	53 ± 2	52 ± 2	56 ± 3	56 ± 4	55 ± 4
Tuber	foot down	45 ± 3	46 ± 2	48 ± 3	35 ± 7	45 ± 4
ischiadicum	lift off	46 ± 3	46 ± 2	48 ± 3	53 ± 5	50 ± 4
hip joint	foot down	47 ± 2	47 ± 1	51 ± 3	42 ± 5	48 ± 3
	lift off	47 ± 2	47 ± 1	51 ± 2	51 ± 8	52 ± 5
knee joint	foot down	38 ± 3	36 ± 3	37 ± 3	43 ± 4	40 ± 3
	lift off	19 ± 3	23 ± 3	25 ± 4	21 ± 4	23 ± 6
ankle joint	foot down	4 ± 1	5 ± 1	6 ± 1	5 ± 2	7 ± 2
	lift off	23 ± 4	22 ± 2	24 ± 3	28 ± 4	25 ± 2
metatarso-	foot down	2 ± 0	1 ± 1	2 ± 0	1 ± 1	3 ± 1
phalangeal joint	lift off	10 ± 4	7 ± 2	9 ± 2	7 ± 4	7 ± 4
proximal	foot down	4 ± 0	4 ± 1	4 ± 1	5 ± 1	4 ± 1
interphalangeal joint	lift off	5 ± 1	4 ± 1	5 ± 2	6 ± 3	5 ± 1

Discussion

On a treadmill, animals perform only a portion of their locomotion repertoire. Treadmill locomotion or restrained locomotion can be different from that on a normal ground (unrestrained locomotion), as described, e. g., in horses (Barrey et al. 1993) and humans (Elliot and Blanksby 1976). Our present observations of unrestrained locomotion during force plate recordings on *Tupaia glis* at gallop show that the limbs are more extended than on the treadmill, the animal jumps higher and gains longer distances during the swing phase (0.3 m–0.4 m). However, only locomotion on the treadmill allows to analyse kinematics properties using cineradiography, and especially to record series of steps.

Jenkins (1974 a) primarily investigated movements of the distal elements in his study on tree-shrew locomotion. His results were based on a small number of observations. He reported only one value for each of the analysed angles during exploratory activity of the animal. During bounding runs, he analysed only the hindlimbs; no data were given for the forelimbs. Only a detailed analysis of many steps, however, allows to recognise and assess the degree of variability or stereotype of parameters in locomotion. A major deficiency in Jenkins' work (1971, 1974 a) is his neglect of the scapula, which contributes to body propulsion of up to more than 40 % in *T. glis* and more than 60 % in other mammals.

According to Jenkins (1974 a), rhythmic flexions and extensions restricted to the intervertebral articulations between Th11 and L1 occur during exploratory activity and bounding run: "... the lumbar series remains rigid and [does] not contribute to even the most extreme flexion observed". His observations are in sharp contrast to ours on *Tupaia* but also on other small mammals. We found movements in the caudal thoracic spine, but the highest intervertebral amplitudes occur in the lumbar region. The sagittal lumbar spine movements in *Procavia capensis* (Fischer 1994) and *Ochotona rufescens* (Fischer and Lehmann 1998) contribute extensively to body propulsion during in-phase gaits. 'Pelvic movement' during symmetrical gaits in *T. glis* is low compared to other small mammals (*P. capensis* < 20°, Fischer 1994; *Monodelphis domestica* 9°, unpubl. obs.). Most other studies consider only angles of larger segments of the vertebral column to the horizontal line (e. g., Jenkins 1974 a; Heckner 1982; Hurov 1987). Fischer (1994) calculated intervertebral joint angles between reconstructed foot down and lift off positions on freshly dead or anaesthetised animals. The present study is the first cineradiographic analysis that measured sagittal spinal movements in intervertebral joints in animals.

Tupaia is comparable to other small mammals in its limb geometry (Fischer and Lehmann 1998). Especially at gallop we found almost right angles in shoulder, elbow, hip, and knee joint. Limb segments that are in horizontal orientation at foot down or lift off may contribute with their whole length to step length. Such a positioning is found in: *Didelphis virginia* (Jenkins 1971), *Rattus norvegicus* (Jenkins 1974 b), *Procavia capensis* (Fischer 1998), *Ochotona rufescens* (Fischer and Lehmann 1998), *Eulemur fulvus* (Schmidt and Fischer 1999) for humerus and tibia at foot up and for femur at foot down. In *T. glis*, the ulna is also nearly parallel to the ground at foot down during symmetrical gaits.

In *Tupaia* and those other animals so far analysed with the 'overlay method' (*O. rufescens*, Fischer and Lehmann 1998; *Eulemur fulvus*, Schmidt and Fischer 1999) scapular movements contribute substantially to body propulsion (*T. glis*: 42 %–43 %, *O. rufescens*: 67 %, *E. fulvus*: 63 %). Contribution of the humerus ante- and retroversion is comparable between these animals (*O. rufescens*: 21 %, *E. fulvus*: 31 %). In *T. glis*, the effects of humerus movements are different during symmetrical gaits (17 %) from gallop (45 %). The ulna contributes 32 % to body propulsion because of the large extension in the elbow joint at the end of stance during symmetrical gaits, but only 3 % at gallop. The contribution of the hand is similar during all gaits (9 %) and larger in *Tupaia* than in other ani-

mals (*E. fulvus*: 1 %, *O. rufescens*: 3 %). In the hindlimb, propulsive effects of the segments change with gaits, caused by the additive sagittal spine movement at gallop. Spinal contribution is low during symmetrical gaits (2 %) and high (42 %) at gallop. The femur contributes 49% and the foot 21 % to propulsion at gallop. The animal looses some stance length through the movements of the tibia. In *O. rufescens*, sagittal spine movements contribute the major component to propulsion (55 %–65 %) during in-phase gaits, followed by the tibia (19 %–35 %), femur (8 %–10 %) and foot (4 %–7 %).

HEGLUND and TAYLOR (1988) postulated size-related modes of acceleration. Small mammals should increase step frequency and larger animals step length, but step frequency should remain nearly constant even with increasing speed during in-phase gaits. *Tupaia glis* belongs to intermediate forms as well as *Procavia capensis* (FISCHER 1998) and *Eulemur fulvus* (SCHMIDT and FISCHER 1999), which increase both parameters. An increase in step duration and length is reported for *Rattus norvegicus* (COHEN and GANS 1975). Increase of step frequency is attained by abbreviation of the stance phase (hindlimbs of *T. glis*; *E. fulvus*, SCHMIDT and FISCHER 1999; *Loris tardigradus*, *Nycticebus coucang*, DEMES et. al. 1990; *Macaca mulatta*, *Felis catus*, humans, VILENSKY and GEHLSEN 1984), of the swing duration (*Dasyuroides byrnei* at in-phase gaits, KÜHNAPFEL 1996) or both parameters (forelimbs of *T. glis*; *R. norvegicus,* COHEN and GANS 1975; *P. capensis*, FISCHER 1998). JENKINS (1974 a) described a shortening of the stance duration without differences in the footfall pattern during symmetrical gaits (v = 1.5m/s–1.75 m/s). Swing duration seems to be increased (JENKINS 1974 a), but no details were given. In the present study, a decrease of the stance duration up to 75 % was found during symmetrical gaits; at gallop step frequency is almost constant.

All mammals analysed so far have speed independent swing durations (COHEN and GANS 1975; ELLIOT and BLANKSBY 1976; VILENSKY and GEHLSEN 1984; HOY and ZERNICKE 1985; DEMES et al. 1990; VAN WEEREN et al. 1993; FISCHER 1994; KÜHNAPFEL 1996; SCHMIDT and FISCHER 1999). The measured values for *Tupaia* are in the range of animals of comparable size (70 ms–140 ms).

A remarkable result is the almost constant horizontal distance between the scapular fulcrum and the finger tips at foot down (symmetrical gaits: 68 ± 4 mm, gallop: 62 ± 7 mm). In contrast to this, JENKINS (1974 a) figured foot down beneath the shoulder joint. Such a positioning of the foot seems to be a speciality of exploratory activity, but is never observed at faster gaits. Also in *Monodelphis domestica* and *Dasyuroides byrnei*, the distance between the fulcrum of the scapula and finger tips scatters only slightly (*M. domestica*: 35 ± 3 mm, N = 34; *D. byrnei*: 32 ± 5, N = 19; own observ.). Foot down is below the eye point in *T. glis*, *M. domestica*, *D. byrnei* as well as in *Galea musteloides*, *Rattus norvegicus* (unpubl. observ.) and *Ochotona rufescens* (FISCHER and LEHMANN 1998). In contrast, the point of foot down lies in front of the eyes in *Eulemur fulvus* (SCHMIDT and FISCHER 1999) which has elongated limbs.

The onsets of the various flexion and extension movements are not synchronous with foot down and lift off. The movements of nearly all joints on the fore- and hindlimb start before foot down or lift off in *Tupaia glis.* A beginning of scapula retroversion well before foot down was also described for *Procavia capensis* (FISCHER 1994), *Felis catus* (BOCZEK-FUNCKE 1996), *Ochotona rufescens* (FISCHER and LEHMANN 1998), *Eulemur fulvus* (SCHMIDT and FISCHER 1999), *Dasyuroides byrnei*, *Monodelphis domestica* (unpubl. observ.). In contrast, anteversion of the scapula begins at different times e. g., in the last quarter of stance (*T. glis*, *E. fulvus*, *F. catus*, *M. domestica*) or at lift off (*P. capensis*, *Cercopithecus aethiops* (WHITEHEAD and LARSON 1994). Retroversion before foot down could reduce deceleration forces (FISCHER 1994). Measurements of ground reaction forces prove that deceleration forces in *T. glis* are relatively small (unpubl. observ.).

For the first time, a gait-dependent kinematic behaviour of a limb joint is observed. During symmetrical gaits, the shoulder joint movements in *Tupaia* comprise two flexions

and two extensions per step. Only one flexion and one extension occur at gallop. With change of gaits, shoulder joint movements are reduced from a biphasic to a monophasic pattern.

The works of Whitehead and Larson (1990) and Schmidt and Fischer (1999) are the only cineradiographic studies on primate locomotion (*Cercopithecus aethiops* and *Eulemur fulvus*, respectively) available at present. Shoulder joint amplitudes are significantly larger in the terrestrial *C. aethiops* than in small non-primates. A remarkable scapular movement was described for *E. fulvus*, including a distinct mediad rotation. Both species as well as other primates have elongated limbs. *Tupaia glis* does not share these features with primates. The locomotion of *T. glis* is similar to that of other small mammals in its kinematic and metric parameters. It appears that these parameters are common in mammals of a small to medium size class, independent of their taxonomic group.

In all analysed small to medium-sized mammals body propulsion is mainly achieved by actions of the proximal limb segments. The flexed limb posture enables the animal to react to obstacles and reduce vertical displacement of the centre of gravity. The horizontal orientation of the upper arm and lower leg at lift off, and the upper leg at foot down seem to be standard parameters of the locomotion of small mammals. Additive sagittal spine movements contribute substantially to body propulsion during in-phase gaits. All these features probably occurred in the most recent common ancestor of therian mammals.

Acknowledgements

We are indebted to Prof. Dr. H.-R. Duncker (Gießen) and Prof. Dr. H.-J. Kuhn (Göttingen) for kindly providing us with the animals. We thank Dr. D. Haarhaus and his staff (IWF Göttingen) for their patience and competence in cineradiography. We also thank all members of our working group in Jena for many discussions, and especially Dr. A. Haas (Jena) and PD Dipl. Ing. Dr. Med. H. Witte (Jena) for thoroughly revising the manuscript. M. Roser (Jena) skilfully helped with the illustrations. This research was supported by the Deutsche Forschungsgemeinschaft (DFG) (Fi 410/ 1–3; Innovationskolleg "Bewegungssysteme", Teilprojekt B 1).

Zusammenfassung

Kinematische Analyse der Fortbewegung von Tupaia glis (Scandentia: Tupaiidae) auf dem Laufband

Mit Hilfe der Röntgenkinematographie wurde die Fortbewegung von *Tupaia glis* auf dem Laufband in verschiedenen Gangarten (Schritt, Trab und Galopp) untersucht. *T. glis* erhöht seine Geschwindigkeit in den symmetrischen Gangarten (Schritt, Trab) durch eine Steigerung der Schrittfrequenz, im Galopp wird durch eine Flugphase Schrittlänge gewonnen. Die Vorderextremität fußt in allen Gangarten unter dem Auge auf, der Abfußpunkt liegt in den symmetrischen Gangarten hinter und im Galopp meist vor dem Lot des Scapula-Drehpunktes. Humerus und Tibia werden beim Abfußen in allen Gangarten horizontal positioniert. Beim Auffußen wird das Femur parallel zum Untergrund gestellt. Die proximalen Extremitätenabschnitte sind maßgeblich am Rumpfvortrieb beteiligt (Scapula in allen Gangarten: 42–43 %, Femur in den symmetrischen Gangarten: 82 % und im Galopp: 49 %). Im Galopp trägt die additive Sagittalbewegung 42 % zum Vortrieb des Körpers bei. Ellbogen- und Kniegelenk werden in den symmetrischen Gangarten am Ende der Stemmphase deutlich weiter geöffnet (30–40°) als im Galopp. Erstmals konnte ein von der Gangart abhängiger Ablauf der Gelenkbewegungen beobachtet werden. Der biphasische Bewegungsablauf des Schultergelenkes mit zwei Beugungen und Streckungen pro Schrittzyklus in den symmetrischen Gangarten wird auf einen monophasischen Ablauf im Galopp reduziert. Die Dorsal- und Ventralflexionen der Wirbelsäule wurden zum ersten Mal auf der Basis der Röntgenkinematographie untersucht und dabei nachgewiesen, daß es sich im Unterschied zu der bei anderen Säugetieren beschriebenen additiven Lumbalbewegung bei

T. glis um eine additive Thorako-Lumbalbewegung handelt. Die untersuchten kinematischen und metrischen Parameter von *T. glis* stimmen in wesentlichen Punkten mit denen anderer kleiner und mittelgroßer Säugetiere überein. Die Kinematik ist abhängig von der Körpergröße und unabhängig von der systematischen Stellung der Tiere.

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Z. Säugetierkunde **64** (1999) 154–168
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http://www.urbanfischer.de/journals/saeugetier



ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Nahrungspräferenzen der Feldmaus *Microtus arvalis* in der Agrarlandschaft unter Berücksichtigung der Pflanzeninhaltsstoffe

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Eingang des Ms. 13. 10. 1998
Annahme des Ms. 25. 01. 1999

Abstract

Food preferences of the common vole Microtus arvalis in the agricultural landscape with regard to nutritional components of plants

At high population densities the common vole *Microtus arvalis* may cause severe damage to agricultural crops. Knowledge of its food preferences could be used to promote preferred plants in agricultural compensation areas such as fallow fields or weedy borders to crop fields. Thus migration into adjacent fields may be prevented. Since such migrations are more likely to occur in winter, laboratory feeding choice tests were carried out during this season in order to investigate the food choices of the common vole. Feeding signs in the field served for qualitative comparisons. Plant nutritional components (nitrogen, sugar, starch, and phenolics) as well as energy and water content were analyzed and related to plant preferences. Clear preferences emerged from the choice trials. The most preferred plants were *Hordeum vulgare* (leaves), *Brassica napus* (leaves) and *Beta vulgaris altissima* (roots) among cultivated plants, and *Achillea millefolium* (leaves) and *Trifolium pratense* (leaves) among weed strip plants. There was no relationship between preferences and the analyzed nutritional parameters. From the 5 most attractive plants in laboratory tests, feeding signs in the field were observed at high frequency only for *T. pratense* and *B. napus*. *T. pratense* may therefore be suitable for preventing migrations of *M. arvalis* from bordering areas into rape fields.

Key words: *Microtus arvalis*, food preferences, plant nutritional components

Einleitung

Die Feldmaus (*Microtus arvalis* Pallas) besiedelt verschiedenartigstes Kulturland sowie offenes, nicht zu feuchtes Grasland bis oberhalb von 2000 m ü. M. Im größten Teil ihres Verbreitungsgebietes, das sich von Nordspanien bis nach Ostasien erstreckt, spielt sie eine bedeutende Rolle als Ackerschädling (Stein 1958).

Die Intensivierung der Landwirtschaft hat zu einer drastischen biologischen Verarmung der Agrarlandschaft geführt. Ackerkrautstreifen, die als Buntbrache mit einheimischen Wildkräutern seit ca. zehn Jahren auch in der Schweiz in oder am Rande von Feldern angesät werden, erhöhen die Biodiversität der Agrarlandschaft. Als positive Auswirkung wurde nicht nur eine erhöhte Artendiversität verschiedener Arthropodengruppen in den Streifen festgestellt (Lys und Nentwig 1994; Frank und Nentwig 1995 a), sondern auch eine höhere Dichte von Nützlingen in angrenzenden als in weiter entfernten Feldbereichen, was zu niedrigeren Dichten schädlicher Insekten in Streifennähe führt (Lys und Nentwig 1992; Frank und Nentwig 1995 b; Hausammann 1996). Außerdem

0044-3468/99/64/03 – 154 $ 12.00/0

werden die Ackerkrautstreifen von Vögeln zum Nahrungserwerb genutzt (LILLE 1996). Feldmäuse kommen dort mit jahreszeitlichen Schwankungen vor (BAUMANN 1996): Von Mai bis September herrscht eine relativ hohe Populationsdichte, die ab Oktober abnimmt, gegen März ein Minimum erreicht und danach wieder zunimmt. Im Sommer stellte BAUMANN (1996) unmittelbar nach der Getreide- und Hanfernte der angrenzenden Felder eine vorübergehende starke Zunahme der Population von *M. arvalis* in den Streifen fest, was er auf Wanderungen aus den Feldern zurückführte. Dieses wirft die Frage auf, ob sich die Feldmäuse aus den Streifen auf die Suche nach Nahrung in die Felder begeben und insbesondere, ob sie sich hauptsächlich von Kultur- oder Buntbrachepflanzen ernähren. Im Winter sind Wanderungen aus den Streifen in die angrenzenden Felder am wahrscheinlichsten, weil die Streifen in dieser Jahreszeit verminderte Ernährungsmöglichkeiten bieten. Wintergetreide- und Rapsfelder dürften hingegen eine anziehende Wirkung ausüben.

Die Nahrungsaufnahme von *M. arvalis* in Agrarökosystemen unter Berücksichtigung der Wildkräuter ist bisher wenig erforscht. TRUSZKOWSKI (1982) stellte in Getreide- und Rapsfeldern eine Vorliebe für Unkräuter fest; von den 29 vorhandenen Unkrautarten wurden fast alle gefressen, und zwar ohne ausgeprägte Präferenzen. Auf Dauergrünland geht die Feldmaus bei der Nahrungsaufnahme selektiv vor und zeigt deutliche Präferenzen für bestimmte Pflanzenarten (YU et al. 1980; LEUTERT 1983; RINKE 1990). In keiner der oben angeführten Studien zur Nahrungsökologie von *M. arvalis* wurden die Ursachen der dargelegten Präferenzen untersucht. Da die Nahrungspräferenzen der Wühlmäuse von einer Kombination „positiver“ (Nährstoffe, Energie und Wasser) und „negativer“ (Sekundärmetabolite und Fasern) Nahrungseigenschaften abhängig sind (BATZLI 1985), müssten bei solchen Untersuchungen Parameter beider Eigenschaften analysiert werden. Ziel der vorliegenden Arbeit war die Untersuchung der Nahrungswahl von *M. arvalis* in der Agrarlandschaft im Zeitraum Spätherbst-Winter mittels Futterwahlexperimenten im Labor. Als qualitativer Vergleich diente die Untersuchung der Fraßspuren im Feld. Zur Ursachenuntersuchung eventueller Nahrungspräferenzen wurden einige positive und negative Parameter der getesteten Pflanzen analysiert.

Die Fragestellungen lauteten wie folgt: (1) Geht die Feldmaus bei der Nahrungsaufnahme selektiv vor? (2) Welche Buntbrache- bzw. Kulturpflanzen werden bevorzugt? (3) Werden bestimmte Pflanzenorgane vorgezogen? (4) Besteht ein Zusammenhang zwischen den Präferenzen und den analysierten Parametern?

Material und Methode

Mäusefang und Haltungsbedingungen

Die Feldmäuse wurden von Oktober 1997 bis Januar 1998 in zwei Ackerkrautstreifen auf Ackerland in Belp (bei Bern) mit Longworth-Lebendfallen gefangen. Die Haltung erfolgte bei einer Photoperiode von 12 h Licht/12 h Dunkel unter folgenden Temperatur- bzw. Feuchtigkeitsbedingungen: 17–20 °C bzw. 45–60% bis zum 15. 12. 1997 und 10–16 °C bzw. 48–63% danach. Die Feldmäuse wurden einzeln in Makrolonkäfigen (40 × 25 × 15 cm) mit Späne und einem Blumentopf als Unterschlupf gehalten. Mäusezuchtfutter und Wasser standen ad libitum zur Verfügung und dreimal pro Woche wurden zusätzlich Möhren verfüttert.

Futterwahlexperimente
Versuchsanordnung und -ablauf

Es wurden Futterwahlexperimente als sogenannte „Cafeteria-Tests“ durchgeführt. Dabei wird den Tieren die Wahl zwischen verschiedenen Futtertypen gegeben. Durch die konsumierte Menge jedes Futtertyps können Rückschlüsse auf die Nahrungspräferenzen gemacht werden.

Vor Versuchsanfang wurde den Tieren eine Laborangewöhnungszeit von mindestens 20 Tagen gelassen. Es wurden 2 Serien aus je 6 „Cafeteria-Tests" durchgeführt. Die zwei Serien fanden vom 18. 11. bis zum 12. 12. 1997 bzw. vom 24. 1. bis zum 25. 2. 1998 statt. Die einzelnen Tests dauerten um die 40 h und wurden mit einem Abstand von zwei bis zehn Tagen durchgeführt. Serie 1 und 2 unterschieden sich nur in der Auswahl der Pflanzen und nicht in der Versuchsanordnung. Es wurden einige Kulturpflanzen und im Winter häufige Buntbrachepflanzen ausgewählt. In jedem Test wurden den Feldmäusen 2 verschiedene Blatt- und 2 verschiedene Wurzeltypen zur Wahl vorgelegt. In beiden Serien wurden insgesamt je 8 Pflanzenarten bzw. -organe (im Folgenden als 8 Pflanzen bezeichnet) getestet (Tab. 1 a, 1 b). *Trifolium pratense* wird in der vorliegenden Arbeit ausschließlich als Buntbrachepflanze betrachtet, obwohl sie auch kultiviert wird. Für die Tests wurde frisches Pflanzenmaterial verwendet, das am Tag des Tests aus dem Feld geholt wurde. Einzig die Zuckerrüben wurden bereits im Oktober gesammelt und bis zur Verwendung kühl gelagert.

Mit Ausnahme von Test 1 e, für den nur 5 Tiere zur Verfügung standen, wurden alle Tests mit 6 Einzeltieren durchgeführt. Für jeden Test wurden 6 (für 1 e nur 5) Makrolonkäfige (55 × 35 × 20 cm) neu vorbereitet: Der Boden wurde mit Haushaltpapier bedeckt, vier 14 × 8 × 4 cm große Plastikfutternäpfe (je einer pro Futtersorte) wurden nebeneinander gestellt und dazwischen Metalltrennwände (15 × 11 cm) befestigt.

Das gesammelte Pflanzenmaterial wurde gewaschen. Vier fast gleiche Portionen (zwischen 20 und 40 g je nach Test) wurden abgewogen (Frischgewicht Anfang, FGa) und in die vier Futternäpfe jedes Käfigs gelegt. Die Verteilung der vier Pflanzen auf die vier Futternäpfe jedes Käfigs wurde so gewählt, daß am Ende jeder Serie jede Pflanze möglichst gleich oft in jeder der 4 Positionen angeboten worden war. Von jeder der vier Pflanzen wurde zusätzlich eine Probe bei 50 °C getrocknet und an-

Tabelle 1 a. Versuchsanordnung der „Cafeteria-Serie" 1. Für jeden der 6 „Cafeteria-Tests" (1 a–1 f) sind die 4 getesteten Pflanzen angegeben (X); b): Versuchsanordnung der „Cafeteria-Serie" 2. Für jeden der 6 „Cafeteria-Tests" (2 a–2 f) sind die 4 getesteten Pflanzen angegeben (X).

a

No. Cafeteria Test	Pflanzenarten und -organe							
	Oenothera biennis Rosettenbl.	*Oenothera biennis* Wurzel	*Silene alba* Rosettenbl.	*Silene alba* Wurzel	*Trifolium pratense* Blätter	*Beta vulgaris altissima* Rübe	*Brassica napus* Blätter	*Dipsacus fullonum* Wurzel
1 a	×	×	×	×				
1 b	×	×			×	×		
1 c	×	×					×	×
1 d					×	×	×	×
1 e			×	×			×	×
1 f			×	×	×	×		

b

No. Cafeteria Test	Pflanzenarten und -organe							
	Brassica napus Blätter	*Brassica napus* Wurzel	*Hordeum vulgare* Blätter	*Verbascum densiflorum* Wurzel	*Leucantheum vulgare* Blätter	*Pastinaca sativa* Wurzel	*Achillea millefolium* Blätter	*Echium vulgare* Wurzel
2 a	×	×	×	×				
2 b	×	×			×	×		
2 c	×	×					×	×
2 d					×	×	×	×
2 e			×	×			×	×
2 f			×	×	×	×		

schließend gewogen, um mit dem Wassergehalt das angebotene Trockengewicht (Trockengewicht Anfang, TGa) zu berechnen. Das nicht verwertete Material jeder Pflanze wurde für die chemischen Analysen getrocknet. Die Feldmäuse wurden gewogen (Gewicht Anfang, Ga) und in die Versuchskäfige gesetzt. Nach Ablauf der Versuchsdauer wurden die Tiere aus den Versuchskäfigen genommen und gewogen (Gewicht Ende, Ge). Die Reste der Pflanzen wurden sortiert, gewogen („Frischgewicht" Ende, FGe: nur in Serie 2), getrocknet und erneut gewogen (Trockengewicht Ende, TGe). Tests, in denen keine Reste einer oder mehrerer Pflanzen übrig geblieben waren, wurden mit einem größeren FGa wiederholt. Wegen der beschränkten Haltungsmöglichkeiten wurden 25 der insgesamt 46 verwendeten Feldmäuse zweimal eingesetzt. In solchen Fällen wurde darauf geachtet, daß mindestens 14 Tage Abstand zwischen den beiden Tests eingeschaltet waren, und daß die zwei Tests keine gemeinsame Pflanze hatten (z. B. 1 a und 1 d in Tab. 1 a).

Präferenzmaß

Als Maß für die Präferenz wurde der „Consumption Index" (CI) nach WALDBAUER (1968) folgendermaßen berechnet: $CI = \frac{K}{G \times D} \times 1000$

wobei K = Trocken- bzw. Frischgewichtskonsum (g), G = (Ga + Ge)/2 = Durchschnittliches Tiergewicht während des „Cafeteria-Tests" (g) und D = Dauer des Tests (h). Der CI wurde sowohl nach dem Trockengewichtskonsum (CI TG) als auch nach dem Frischgewichtskonsum (CI FG) wie folgt berechnet:

$$CI\,TG = \frac{TGa - TGe}{G \times D} \times 1000 \qquad CI\,FG = \frac{TGa - TGe}{G \times D} \times \frac{FGa}{TGa} \times 1000$$

Da in Serie 2 die Pflanzenreste auch vor dem Trocknen gewogen wurden (FGe), ist deren Wassergehalt bekannt. Um der Tatsache Rechnung zu tragen, daß die Pflanzenteile (v. a. Blätter) während des Versuchs Wasser verlieren, wurde für Serie 2 der CI zusätzlich nach dem durchschnittlichen Frischgewicht (CI FGd) folgendermaßen errechnet:

$$CI\,FGd = \frac{TGa - TGe}{G \times D} \times \frac{1}{\text{durchschnittlicher Anteil Trockenmaße}} \times 1000$$

$$\text{Durchschnittlicher Anteil Trockenmaße} = \text{Mittelwert aus } \frac{TGa}{FGa} \text{ und } \frac{TGe}{FGe}$$

Als Stichprobengrößen ergeben sich 18 CI TG-, 18 CI FG- und (nur in Serie 2) 18 CI FGd-Werte pro getestete Pflanze; lediglich vier Pflanzen aus Serie 1 weisen 17 und nicht 18 CI TG- und CI FG-Werte auf.

Fraßspuren im Feld

Von Oktober 1997 bis Januar 1998 wurde regelmäßig nach Fraßspuren von *M. arvalis* in einem Ausfallraps-, Raps-, Zuckerrüben- bzw. Wintergerstenfeld und in vier Ackerkrautstreifen in Belp gesucht. Zuerst wurde nach Aktivitätszeichen (Laufwege, Kot, Löcher usw.) und dann nach Fraßspuren gesucht. Als Fraßzeichen galten: direkt an der Pflanze an- oder abgefressene Teile, ganze Pflanzen oder Teile davon in Baueingängen, Nahrungshäufchen auf Laufwegen. Mitte Juni wurden das Raps- und Gerstenfeld erneut nach Aktivitäts- und Fraßzeichen abgesucht. Hierbei wurde darauf geachtet, ob die im Winter festgestellten Vegetationsschäden im Rapsfeld noch erkennbar waren.

Chemische Analysen der Pflanzen

Die für die Analysen getrockneten Pflanzenproben wurden mit einem Mixer zu feinem Pulver gemahlen, in luftdichte Gläschen abgefüllt und danach im Dunkeln bei Raumtemperatur aufbewahrt. Die Analysen erfolgten folgendermaßen: Energiegehalt: Die Bestimmung des Energiegehalts erfolgte mit einem Calorimeter mit einer Einwaage von ca. 1 g und Benzoesäure als Kontrollstandard. Gesamtstickstoff: Der Stickstoffgehalt wurde mit einem Stickstoffanalysator bestimmt. Die Einwaage betrug

ca. 1 g und als Kontrollstandard diente L-Asparaginsäure. Stärke und lösliche Zucker: Die freien Zucker wurden aus 100 mg Pulver mit 0,2 M HCl extrahiert. Für die Stärkebestimmung wurde der zentrifugierte Rückstand zweimal mit Wasser gewaschen und mit 1,5 M Perchlorsäure hydrolysiert. Als Nachweismethode diente der Anthrontest. Die optische Dichte wurde bei 623 nm gemessen und mit Fructose- bzw. Glucosestandards verglichen (MÜLLER-FERCH und MOUCI 1995).

Lösliche Phenole: Die Phenole wurden aus 1 g Pulver unter Rückflußkochen mit Methanol/H_2O 2:1 (v/v) extrahiert. Das Folin-Ciocalteus Phenolreagenz diente als Nachweisreagenz. Die optische Dichte wurde bei 675 nm gemessen und mit Gallussäurestandards verglichen (SCEHOVIC 1990).

Von jeder der 16 getesteten Pflanzen standen drei Proben für die Analysen zur Verfügung (je eine pro „Cafeteria-Test"); für jede Pflanze wurden somit 3 unabhängige Werte pro Parameter bestimmt.

Datenauswertung

Der Durbin-Rang-Test diente zum Nachweis eines globalen signifikanten Unterschieds zwischen den „Consumption Indices" der acht Pflanzen jeder „Cafeteria-Serie". Es wurde dieser Test verwendet, weil a) die Versuchsanordnung einem „incomplete block design" entspricht, b) keine Normalverteilungen als Voraussetzung für parametrische Tests vorlagen. Bei einem „incomplete block design" wird nicht jeder Block (hier 6 Tiere) allen Behandlungen (hier 8 Pflanzen) sondern nur einem Teil davon (hier 4 Pflanzen) unterzogen. Der Tukey-Test diente zur Bestimmung der signifikanten Unterschiede (MARASCUILO und MCSWEENEY 1997). Für jede Pflanze wurde aus den entsprechenden drei Tests der durchschnittliche Rang berechnet. Zur Überprüfung auf Korrelationen zwischen den durchschnittlichen Rängen, die auf dem CI TG, CI FG und CI FGd basieren, wurde der Spearman-Rang-Korrelationskoeffizient berechnet. Der Wilcoxon-Paardifferenzen-Test diente zum Vergleich der „Consumption Indices" der Blätter mit jenen der Wurzeln. Unterschiede bezüglich der Nahrungsbestandteile zwischen Blättern und Wurzeln bzw. Kultur- und Buntbrachepflanzen wurden mit dem Mann-Whitney-U-Test auf Signifikanz geprüft.

Ergebnisse

Futterwahlexperimente: Präferenzen

In Serie 1 zeigten die Feldmäuse sowohl auf der Grundlage vom CI TG als auch vom CI FG signifikant unterschiedliche Präferenzen (Durbin-Test: $\chi^2 = 56{,}16$ für den CI TG, $\chi^2 = 66{,}80$ für den CI FG; df = 7, p < 0,001 für beide Tests; Abb. 1 a). Die durchschnittlichen Ränge der Pflanzen, die auf dem CI TG basieren, waren stark mit jenen korreliert, die auf dem CI FG basieren (Spearman-Rang-Korrelation, $r_s = 0{,}98$, N = 8, p < 0,001). *Brassica napus*, *Trifolium pratense* und *Beta vulgaris* waren sehr beliebt. Die restlichen fünf Pflanzen wurden hingegen wenig bis kaum gefressen. Als besonders unbeliebt zeigten sich die Rosettenblätter von *Oenothera biennis.*

In Serie 2 stellten sich sowohl hinsichtlich des CI TG als auch des CI FG (Abb. 1 b) und CI FGd ebenfalls signifikant unterschiedliche Präferenzen heraus (Durbin-Test: $\chi^2 = 83{,}36$ für den CI TG, $\chi^2 = 83{,}94$ für den CI FG, $\chi^2 = 82{,}27$ für den CI FGd; df = 7, p < 0,001 für alle drei Tests). Auf eine Darstellung des CI FGd wurde in Abb. 1 b verzichtet, weil die Signifikanzen (Tukey-Test) wie jene der ersten Darstellung (CI TG) waren. Es ergab sich eine sehr starke Korrelation zwischen den durchschnittlichen Rängen der Pflanzen, die auf dem CI TG bzw. CI FG bzw. CI FGd beruhen (Spearman-Rang-Korrelation, $r_s = 0{,}99$, N = 8, p < 0,001 zwischen dem CI TG und dem CI FG bzw. CI TG und CI FGd bzw. CI FG und CI FGd). *Hordeum vulgare*, *B. napus* (Blätter) und *Achillea millefolium* waren sehr beliebt. Die übrigen fünf Pflanzen wurden hingegen wenig bis kaum gefressen. Als besonders unbeliebt zeigte sich *Verbascum densiflorum.*

In beiden Serien waren zwei der drei sehr beliebten Pflanzen Kulturpflanzen. Die einzige den zwei Serien gemeinsame Pflanze (*Brassica napus* Blätter) rangierte in beiden Serien hoch oben in der Präferenzrangfolge. Unter den Buntbrachepflanzen erwies sich

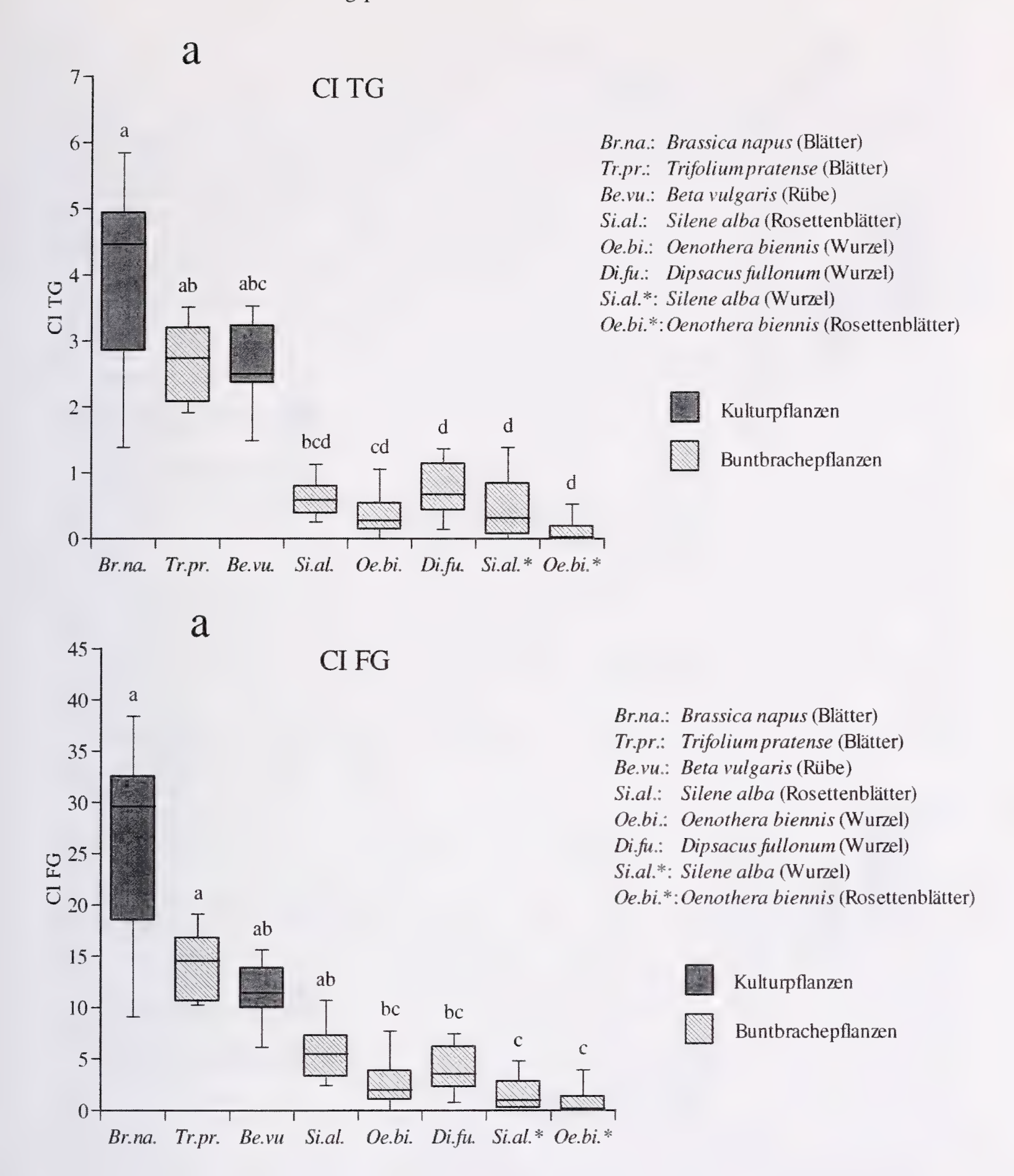


Abb. 1 a: „Consumption Indices" auf der Grundlage vom Trockengewicht (CI TG) bzw. Frischgewicht (CI FG) der acht in Serie 1 getesteten Pflanzen. Die Box-Plots zeigen die 10%-, 25%-, 50%-(Median); 75%- und 90%-Quantile (N = 17 bzw. N = 18). Stichproben von Box-Plots mit gemeinsamen Buchstaben unterscheiden sich nicht signifikant voneinander (Tukey-Test, $p > 0{,}05$).

nur *T. pratense* bzw. *A. millefolium* als besonders attraktiv, während sich alle anderen gegen Ende der Präferenzreihenfolge befanden.

Auch unterschiedlichen Pflanzenorganen gegenüber verhielt sich *M. arvalis* selektiv und fraß signifikant mehr an Blättern als an Wurzeln (Wilcoxon-Paardifferenzen-Test, $p < 0{,}001$ für beide Serien).

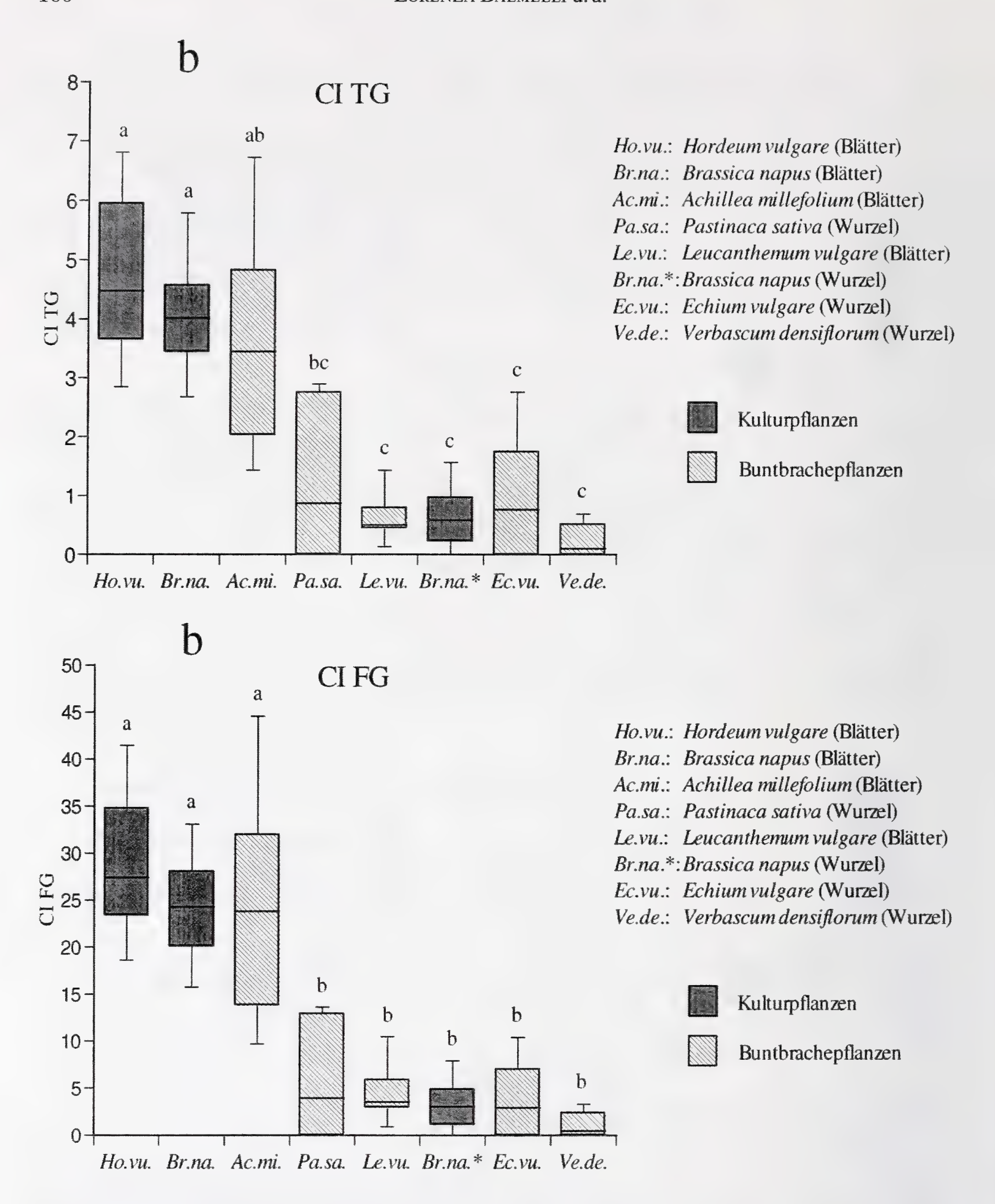


Abb. 1b: „Consumption Indices" auf der Grundlage vom Trockengewicht (CI TG) bzw. Frischgewicht (CI FG) der acht in Serie 2 getesteten Pflanzen. Die Box-Plots zeigen die 10%-, 25%-, 50-(Median), 75%- und 90%-Quantile (N = 18). Stichproben von Box-Plots mit gemeinsamen Buchstaben unterscheiden sich nicht signifikant voneinander (Tukey-Test, p > 0,05).

Fraßspuren im Feld

Im Feld wurden Fraßspuren an insgesamt 24 Pflanzenarten beobachtet. Die verschiedenen Pflanzenarten bzw. -organe ließen sich je nach Fraßhäufigkeit in vier Kategorien einteilen (Tab. 2). Unter den am häufigsten (Kategorien 3 und 2) angefressenen Pflanzen befanden sich folgende Arten und Organe: *Silene alba* (alle vorhandenen Organe mit Ausnahme der Wurzeln), *Brassica napus* (Blätter), *Verbascum densiflorum* (Wurzel), *Melilotus officinalis* (Wurzel), *Agrostemma githago* (Samen), *Trifolium pratense* (Blätter), *Dipsacus fullonum* (Wurzel). Die Fraßspuren an *B. napus* im Winter waren besonders auffällig. Im Rapsfeld hatte *M. arvalis* auf zahlreichen größeren Flächen an den meisten Pflanzen die Blätter am Stiel abgefressen. Die Beweise, daß es sich dabei um Feldmäuse handelte, waren Laufwege mit Kot sowie Rapsblätter in Baueingängen rundherum. Bei der späteren Kontrolle im Juni wurden im Rapsfeld weder Aktivitäts- noch Fraßzeichen entdeckt und die im Winter festgestellten Vegetationsschäden waren nicht mehr erkennbar. Viele Pflanzenarten bzw. -teile wurden nur selten angefressen (Kategorie 1).

An *Beta vulgaris*, *Hordeum vulgare* und *Echium vulgare* konnten im Feld keine Fraßzeichen beobachtet werden. Das Gerstenfeld war auch im Juni unbeschädigt. In folgenden Fällen stimmen die Nahrungspräferenzen, die sich aus den Tests ergaben, nicht mit jenen überein, die aufgrund der Fraßhäufigkeiten im Feld resultierten: *S. alba* (Rosettenblätter), *V. densiflorum* und *D. fullonum* schienen im Feld beliebter zu sein als in den Laborversuchen. Umgekehrt erwiesen sich *H. vulgare*, *B. vulgaris* und *Achillea millefolium* in den Wahlversuchen viel attraktiver als im Feld. Im Falle von *B. vulgaris* dürfte es sich jedoch um eine Fehleinschätzung handeln, da beim Ernten des Feldes viele Feldmäuse zum Vorschein kamen (Gygli, pers. Mitt.). Die Tiere hatten dort wahrscheinlich Fraßschäden angerichtet, die aber nicht entdeckt wurden.

Beim Vergleich von Blättern mit Wurzeln kam im Feld die im Labor festgestellte Vorliebe für Blätter nicht zum Vorschein.

Nahrungskomponenten

Die Werte der untersuchten Komponenten sind in Tabelle 3 zusammengestellt. Werden die zwei Serien zusammen betrachtet, ergibt sich in der Variabilität der einzelnen Parameter folgendes Bild: Phenole, lösliche Zucker und Stärke waren die am stärksten variierenden Parameter. Die größte Variation ergab sich im Phenolgehalt: Die Rosettenblätter von *Oenothera biennis* hatten einen ca. 20fach größeren Wert als die Wurzel von *Beta vulgaris*, *Silene alba*, *Pastinaca sativa* und *Brassica napus*. *S. alba* (Rosettenblätter) hatte mit 9,7% den niedrigsten, *B. vulgaris* mit 67,4% den höchsten Zuckergehalt. *P. sativa* war mit 7,7% besonders reich und *Trifolium pratense* mit 2,0% besonders arm an Stärke. Abgesehen von *B. vulgaris* bestanden zwischen den Pflanzen nur mäßige Unterschiede im Stickstoffgehalt; im Durchschnitt lagen die Werte um 3,5%. Die Werte des Energie- und Wassergehalt, zeigten die kleinste Variation und lagen um 17,5 kJ bzw. 80%.

Blätter waren signifikant reicher an Energie und Stickstoff (Mann-Whitney-U-Test, $p < 0,01$) sowie an Wasser und Phenolen ($p < 0,05$) als Wurzeln. Wurzeln enthielten hingegen signifikant mehr Zucker ($p < 0,001$) und tendenziell auch mehr Stärke ($p = 0,059$). Zwischen Kultur- und Buntbrachepflanzen bestand hingegen bezüglich keiner der Komponenten ein signifikanter Unterschied ($p > 0,05$).

Für einen Vergleich der „Consumption Indices" mit den untersuchten Parametern müssen Serie 1 und 2 getrennt betrachtet werden. Der Vergleich der Werte der Nahrungsbestandteile der drei Pflanzen mit dem höchsten CI mit jenen der restlichen fünf läßt in keiner Serie eine Tendenz erkennen, Pflanzen mit einem höheren Gehalt an positiven Komponenten (Wasser, Energie, Stickstoff, Zucker, Stärke) bzw. mit einem niedrigeren Phenolgehalt zu bevorzugen.

Tabelle 2. Pflanzenarten und -teile, an denen im Feld keine bzw. selten bis sehr oft Fraßspuren beobachtet wurden. Die Einteilung in die vier Spalten beruht auf der Häufigkeit, mit der Fraßspuren beobachtet wurden: 0 = nie, 1 = selten (1–33% der Feldinspektionen), 2 = oft (34–67%), 3 = sehr oft 68–100%). Unter 0 sind nur in Wahlversuchen verwendete Pflanzen aufgeführt. C1, C2: in „Cafeteria-Serie“ 1 bzw. 2 verwendet. Als Vergleich ist für jede „Cafeteria-Pflanze“ der durchschnittliche Rang auf der Grundlage vom CI FG („Consumption Index“ nach dem Frischgewicht) angegeben.
*: Beobachtungen, die nur am Anfang der Untersuchungsperiode gemacht wurden, da diese Pflanzen bzw. Pflanzenteile im Spätherbst entweder absterben oder geerntet werden.

0	**1**	**2**	**3**
C1 *Beta vulgaris* (Rübe)* 2,0	C1 *Oenothera biennis* (Wurzel) 2,8	C1 *Trifolium pratense* (Stengel mit Blättern) 1,4	C1 *Silene alba* (Blattrosette) 2,2
C2 *Hordeum vulgare* (Blätter) 1,2	C1 *Silene alba* (Wuzel) 3,6	C1 *Dipsacus fullonum* (Wurzel) 3,1	C1/C2 *Brassica napus* (Blätter mit Stiel) 1,4/1,2
C2 *Echium vulgare* (Wurzel) 3,3	C1 *Oenthera biennis* (Blattrosette) 3,5	*Triticum aestivum* (Körner aus den Ähren)*	C2 *Verbascum densiflorum* (Wurzel) 3,6
	C2 *Brassica napus* (Wurzel) 3,1	*Plantago major* (Blattrosette)*	*Melilotus officinalis* (Wurzel und Stengelbasis)*
	C2 *Achillea millefolium* (Blätter) 1,7	*Foeniculum vulgare* (Wurzel und Stengelbasis)*	*Silene alba* (Stengel mit Blättern)*
	C2 *Pastinaca sativa* (Wurzel) 2,9	*Poa trivialis* (Halme)*	*Silene alba* (Samenkapseln)*
	C2 *Leucanthemum vulgare* (Blätter) 2,9	*Papaver rhoeas* u. *P. somniferum* (Samenkapseln)*	*Agrostemna githago* (Samenkapseln und Samen)*
	Melilotus officinalis (Stengel mit Blättern)*	*Tussilago farfara* (Blütenknospen und Wurzel)	
	Lolium multiflorum (Ähre)*		
	Medicago sativa (Stengelbasis)*		
	Anthemis tinctoria (Stengel mit Blättern)*		
	Plantago lanceolata (Blattrosette)		
	Onobrychis viciifolia (Stengel mit Blättern)		
	Centaurea jacea (grundständige Blätter)		

Tabelle 3. „Consumption Indices“ nach dem Frischgewicht (CI FG) und untersuchte Komponenten der getesteten Pflanzen. Für jede Serie sind die Pflanzen nach abnehmendem Median CI FG aufgeführt. Die Nahrungsbestandteile sind als Mittelwerte ± Standardabweichung angegeben und beziehen sich, mit Ausnahme des Wassergehalts, auf die Trockenmasse. Mittelwerte der beiden Serien für Blätter und Wurzeln sowie für Kultur- und Buntbrachepflanzen sind zusätzlich am Ende der Tabelle angegeben.

Pflanzenarten und -organe	Medien CI FG	Wasser (%)	Energie (kJ/g org. Subst.)	Stickstoff (%)	Zucker (%)	Stärke (%)	Phenole (%)
Serie 1							
Brassica napus (Blätter)	29,63	84,8 ± 0,1	18,1 ± 0,1	4,0 ± 0,2	30,8 ± 1,0	2,7 ± 0,1	2,3 ± 0,1
Trifolium pratense (Blätter)	14,56	81,1 ± 0,4	18,9 ± 0,2	3,8 ± 0,1	16,0 ± 0,3	2,0 ± 0,1	4,1 ± 0,8
Beta vulgaris (Rübe)	11,43	77,2 ± 0,8	16,8 ± 0,1	0,9 ± 0,0	67,4 ± 0,2	2,5 ± 0,0	0,6 ± 0,0
Silene alba (Rosettenblätter)	5,48	89,0 ± 1,2	17,9 ± 0,1	4,3 ± 0,1	9,7 ± 1,2	3,6 ± 0,2	4,5 ± 0,8
Dipsacus fullonum (Wurzel)	3,57	81,7 ± 0,3	16,9 ± 0,1	2,1 ± 0,1	44,9 ± 0,6	3,2 ± 0,1	2,1 ± 0,2
Oenothera biennis (Wurzel)	2,01	86,6 ± 0,3	15,9 ± 0,1	2,9 ± 0,1	42,8 ± 0,8	3,4 ± 0,1	5,7 ± 0,2
Silene alba (Wurzel)	1,02	70,5 ± 0,8	16,6 ± 0,1	2,1 ± 0,1	48,6 ± 1,8	3,8 ± 0,5	0,8 ± 0,0
Oenothera biennis (Rosettenblätter)	0,19	86,5 ± 0,1	17,1 ± 0,1	3,5 ± 0,1	23,1 ± 1,1	3,3 ± 0,3	10,9 ± 0,4
Serie 2							
Hordeum vulgare (Blätter)	27,42	84,2 ± 0,8	18,7 ± 0,2	4,3 ± 0,3	25,1 ± 1,8	4,2 ± 0,9	1,5 ± 0,0
Brassica napus (Blätter)	24,26	82,9 ± 0,9	18,6 ± 0,2	4,4 ± 0,1	25,5 ± 2,2	2,7 ± 0,1	1,9 ± 0,0
Achillea millefolium (Blätter)	23,79	85,3 ± 0,3	17,8 ± 0,1	3,7 ± 0,1	25,5 ± 1,8	3,1 ± 0,3	3,7 ± 0,1
Pastinaca sativa (Wurzel)	3,96	79,5 ± 0,9	17,0 ± 0,03	2,7 ± 0,2	53,4 ± 0,2	7,7 ± 1,8	0,4 ± 0,0
Leucanthemum vulgare (Blätter)	3,55	86,0 ± 0,6	18,1 ± 0,04	4,0 ± 0,2	21,4 ± 1,5	2,7 ± 0,1	3,6 ± 0,0
Brassica napus (Wurzel)	3,04	80,6 ± 0,6	17,6 ± 0,1	3,9 ± 0,1	37,0 ± 1,8	3,9 ± 0,1	0,6 ± 0,0
Echium vulgare (Wurzel)	2,93	74,3 ± 0,5	16,6 ± 0,03	2,7 ± 0,2	55,8 ± 2,9	6,5 ± 1,0	1,4 ± 0,2
Verbascum densiflorum (Wurzel)	0,47	78,5 ± 0,6	17,2 ± 0,1	3,4 ± 0,1	43,5 ± 0,6	4,3 ± 1,7	2,1 ± 0,1
Blätter		85,0 ± 2,4	18,2 ± 0,6	4,0 ± 0,3	22,1 ± 6,5	3,0 ± 0,7	4,1 ± 3,0
Wurzeln		78,6 ± 4,8	16,8 ± 0,5	2,6 ± 0,9	49,2 ± 9,5	4,4 ± 1,8	1,7 ± 1,8
Kulturpflanzen		81,9 ± 3,1	18,0 ± 0,8	3,5 ± 1,5	37,2 ± 17,6	3,2 ± 0,8	1,4 ± 0,8
Buntbrachepflanzen		81,7 ± 5,7	17,3 ± 0,8	3,2 ± 0,7	35,0 ± 16,1	4,0 ± 1,7	3,6 ± 2,9

Diskussion

Futterwahlexperimente: Präferenzen

Die Ergebnisse der Wahlversuche bestätigen die Erkenntnisse anderer Autoren in der ausgeprägten Selektivität von *M. arvalis* bei der Nahrungswahl (Yu et al. 1980; Leutert 1983; Rinke 1990, 1991). Der Vergleich der mittels „Cafeteria-Tests" festgestellten Präferenzen mit jenen aus anderen Untersuchungen ist jedoch durch folgende Faktoren erschwert: Zur Untersuchung der Nahrungsökologie der Feldmaus wurden bisher verschiedene Methoden angewendet. Die meisten davon weisen bestimmte Schwachpunkte auf. Mageninhalts- bzw. Kotuntersuchungen zeigen nur die Zusammensetzung der letzten Nahrungsaufnahme bzw. führen zur Unterschätzung von leicht verdaulichen Pflanzenteilen wie z. B. fleischigen Wurzeln (Phillipson et al. 1983). Bei der Bestimmung der Artenzusammensetzung von Nahrungsresten werden Pflanzen, die in situ gefressen wurden, nicht erfaßt. Futterwahlexperimente berücksichtigen nicht die relative Ressourcenverfügbarkeit, die eine wichtige Komponente der Nahrungswahl in der Natur ist (Godfrey 1953; Zimmerman 1965; Riewe 1973). Die untersuchten Feldmauspopulationen stammen aus verschiedenen Habitaten (Agrarökosysteme, Fett- bzw. Trockenwiesen usw.), was z. T. zu völlig unterschiedlichen erfaßten Pflanzenarten führt. Zwischen Populationen aus demselben Habitattyp können beträchtliche Unterschiede bezüglich der Nahrungspräferenzen bestehen. Die verschiedenen Studien wurden z. T. zu unterschiedlichen Jahreszeiten durchgeführt. Daraus wird ersichtlich, warum sowohl Übereinstimmungen als auch Diskrepanzen zu Literaturangaben vorliegen können.

In der Folge werden die Ergebnisse der Futterwahlversuche mit den Befunden anderer Autoren, die das Nahrungswahlverhalten von *M. arvalis* quantitativ untersucht haben, verglichen. Es wird nur auf die wenigen gemeinsamen Pflanzenarten eingegangen. In Einklang mit dem sehr niedrigen Median „Consumption Index" von *Leucanthemum vulgare* in dieser Studie konnte Rinke (1990) diese Art nur selten und mit einem sehr geringen Volumenanteil im Mageninhalt nachweisen. Im Gegensatz zu der hier registrierten hohen Attraktivität von *Trifolium pratense* ordnete Rinke (1990) diese Art der Kategorie derjenigen mit minderer Präferenz zu. Die hier ermittelte Attraktivität von *Achillea millefolium* stimmt weder mit den Befunden von Leutert (1983) noch mit jenen von Rinke (1990) überein. Der erstere stellte gegenüber dieser Art Gleichgültigkeit fest und der letztere teilte sie in die Kategorie der Arten mit minderer Präferenz ein. So wie hier signifikant mehr an Blättern gefressen wurde als an Wurzeln, bestand die Diät der von Truszkowski (1982) untersuchten Population oft zu fast 100% aus grünen Pflanzenteilen, während Wurzeln mit einem Anteil von nur 0,1 bis 7,4% in der Diät vorhanden waren. Abgesehen von wenigen Ausnahmen schien *M. arvalis* bei der Wahl zwischen Kultur- und Buntbrachepflanzen erstere vorzuziehen. Im Gegensatz dazu stellte Truszkowski (1982) in Getreide- und Rapsfeldern eine Präferenz für Unkräuter fest. Man muß aber bedenken, daß in der vorliegenden Arbeit nur eine kleine Auswahl von Buntbrachepflanzen berücksichtigt wurde.

Fraßspuren im Feld

Ein sehr artenreiches Nahrungsspektrum der Feldmaus ergab sich auch aus anderen Studien (Yu et al. 1980; Leutert 1983; Rinke 1990; Baumann 1996). In Einklang mit den hier erhobenen Feldbefunden stellte Stein (1958) besonders im Winter starken Fraß an *Trifolium pratense* fest. Die großen Schäden an *Brassica napus* müssen nicht verwundern, da nach Stein (1958) *M. arvalis* in Winterrapsfeldern optimale Lebensbedingungen findet. Raps ist nur im frühen Stadium gefährdet (Stein 1958). Dies erklärt, warum bei der späteren Kontrolle im Juni keine Fraßzeichen entdeckt wurden. Die Tatsache, daß die im

Winter festgestellten Vegetationsschäden im Juni nicht mehr erkennbar waren, läßt sich auf die hohe Regenerationsfähigkeit von Raps zurückführen. Unerwartet war das Fehlen von Fraßzeichen im Gerstenfeld im Juni, da unter den Kulturpflanzen reifendes Getreide am stärksten von diesem Ackerschädling betroffen ist (Stein 1958). Mitte Juni waren die Gerstenkörner noch nicht ganz reif und vielleicht deshalb für die Feldmäuse nicht attraktiv. Nach Stein (1958) ist *Beta vulgaris* wenig begehrt, während hier weder das Vorhandensein noch das Fehlen von Fraßspuren mit Sicherheit behauptet werden kann.

Die Tatsache, daß einige der in den Wahlversuchen verwendeten Pflanzen im Feld beliebter bzw. weniger attraktiv waren als im Labor, läßt sich mit großer Wahrscheinlichkeit auf Faktoren wie z. B. Feinde und Deckung zurückführen, die in den Laborexperimenten unberücksichtigt blieben. So konnten im Feld trotz des sehr hohen „Consumption Index" keine Fraßzeichen an *Hordeum vulgare* beobachtet werden, da sich die Feldmäuse im Winter vermutlich wegen unzureichender Deckung nicht ins Gerstenfeld wagten. *M. arvalis* frißt nur bei guter Deckung (Stein 1958).

Nahrungskomponenten

Die Erwartung bei der Bestimmung einiger Komponenten war, daß nur solche Parameter, die unter den untersuchten Pflanzen eine deutliche Variabilität aufwiesen, eine Rolle bei der Nahrungswahl spielen. Aufgrund dieser Erwartung erwiesen sich nur die Phenole, der Zucker und die Stärke als potentiell wichtig. Angesichts seiner mäßigen Variation zeigte sich der Stickstoffgehalt hingegen als potentiell weniger wichtig. Daß der Wasser- und Energiegehalt nur eine kleine Variation aufwiesen, war vorauszusehen: Einerseits haben Blätter und dicke, fleischige Wurzeln in der Regel eine nicht stark voneinander abweichende prozentuale Trockenmasse und andererseits wurden keine fettspeichernden und somit energiereicheren Organe untersucht.

Die Tatsache, daß in den „Cafeteria-Tests" Blätter einen signifikant höheren „Consumption Index" hatten als Wurzeln, steht mit großer Wahrscheinlichkeit nicht im Zusammenhang mit dem festgestellten signifikanten Unterschied im Gehalt an den untersuchten Komponenten. Vielmehr könnte die in den Wahlversuchen fehlende Deckung die Ursache davon sein: Das Fressen aus den niedrigen und offenen Futternäpfen bzw. auf dem kahlen Käfigboden war den Tieren sicher unangenehm. Deshalb haben sie versucht, das Futter zum unmittelbaren Verzehr möglichst in den Blumentopf zu transportieren. Der kleine Durchmesser des Eingangslochs hat ihnen das Eintragen und somit den Verzehr von Wurzeln stark erschwert. Diese Interpretation würde somit auch erklären, weshalb aufgrund der Fraßspuren im Feld keine Vorliebe für Blätter zum Vorschein kam. Der Vergleich der „Consumption Indices" mit den Werten der analysierten Parameter zeigte, daß zwischen den Präferenzen und diesen Parametern keine Beziehung besteht. Auch in der Mehrheit der bisher durchgeführten Studien zur Nahrungsökologie von Kleinnagern besteht kein Zusammenhang zwischen Präferenzen und dem Gehalt an Kohlenhydraten, Phenolen und Stickstoff. Dies gilt für die Arbeiten von Kopp (1993) und Bozinovic et al. (1997) bezüglich des Kohlenhydratgehalts, für jene von Lindroth und Batzli (1984), Marquis und Batzli (1989), Kopp (1993) sowie Hjälten et al. (1996) bezüglich des Phenolgehalts und für jene von Hjälten et al. (1996) und Murray und Dickman (1997) bezüglich des Stickstoffgehalts. Im Gegensatz dazu fanden Bergeron und Jodoin (1987) sowie Harju und Hakkarainen (1997) eine starke negative Korrelation zwischen Präferenzen und Phenolgehalt, während Marquis und Batzli (1989) und Kopp (1993) eine positive Korrelation zwischen Präferenzen und Stickstoffgehalt feststellten. Das Fehlen einer Beziehung zwischen den hier festgestellten Präferenzen und den analysierten Komponenten heißt aber nicht, daß sich Feldmäuse prinzipiell ohne Rücksicht auf das Vorhandensein bestimmter Nahrungsbestandteile ernähren. Folgendes muß berücksichtigt werden: Phenole sind eine komplexe Gruppe von Sekundärmetaboliten, zu der

mehrere Verbindungen mit vielfältigen Wirkungen auf Herbivore gehören (Lindroth 1989): a) Einfache Phenole und Flavonoide können verschiedene toxische Effekte haben wie z. B. Hemmung der Zellatmung, der Enzymfunktion und des Membrantransports. b) Cumarine können Organläsionen verursachen sowie hämorrhagische und koagulationshemmende Effekte zeigen. c) Tannine wirken infolge oberflächlicher Eiweißfällung auf Haut- und Schleimhautzellen adstringierend. Weiter hemmen sie Verdauungsenzyme, bilden mit Nahrungsproteinen unverdauliche Komplexe und reduzieren die Aktivität der Mikrobenflora des Darmes. d) Lignine hemmen die Verdauung. Daraus geht hervor, daß die Bestimmung der Gesamtphenole ohne jegliche Differenzierung vermutlich nicht ausreicht, um den Effekt dieser vielseitigen Stoffgruppe auf die Schmackhaftigkeit festzustellen. Der Gesamtstickstoffgehalt gibt meistens keine korrekte Schätzung des Proteinanteils an. Stickstoff ist nicht nur in proteinogenen Aminosäuren enthalten, sondern z. B. auch in mehreren Verbindungen unter den Sekundärmetaboliten wie Alkaloiden, Aminen, cyanogenen Glykosiden, Glucosinolaten und nicht proteinogenen Aminosäuren (Lindroth 1989). Es wurden nur einige wenige positive und negative Parameter der Pflanzen bestimmt. Nach Batzli (1985) richten sich Wühlmäuse bei der Nahrungswahl auch nach dem Gehalt an Kalzium, Phosphor, Natrium, Faser, Alkaloiden und Saponinen. Die Verdaulichkeit des Futters für Herbivore ist negativ mit dem Fasergehalt (Hemicellulose, Cellulose, Lignin) korreliert und zu viel Faser kann die Nahrungsaufnahme von Wühlmäusen hemmen (Batzli 1985). Alkaloide und Saponine wirken toxisch (Lindroth 1989). Der Versuch, die Präferenzen der Feldmaus mit wenigen, einzeln betrachteten Nahrungsbestandteilen zu erklären, ist auch deshalb schwierig, weil die Präferenzen vermutlich von einem Komplex interagierender Komponenten bestimmt werden. So können z. B. Giftwirkungen einiger Stoffe durch andere Bestandteile der Nahrung gemildert werden. Die gleichzeitige Aufnahme von Tanninen und Saponinen (im richtigen Verhältnis) mit der Nahrung kann die Absorption der Gifte im Darmtrakt verhindern (Freeland et al. 1985). Natrium ist wahrscheinlich ein limitierendes Element für die Entgiftung von Abwehrstoffen der Futterpflanzen (Hansson 1990). Sollte dies der Fall sein, könnte durch die Bestimmung des Natriumgehalts die Beziehung zwischen Präferenzen und Sekundärmetaboliten aufgeklärt werden. Um die Aufnahme chemischer Abwehrstoffe zu vermeiden, mag die Feldmaus in einigen Fällen Pflanzen mit einem niedrigen Nährwert bevorzugen. In anderen Fällen wird sie Pflanzen mit einem hohen Gehalt an Sekundärmetaboliten vorziehen, weil die Kosten dieser Wahl bei weitem von hohen Nährstoffwerten kompensiert sind.

Die einzige Pflanze, die sich sowohl in den Wahlversuchen (Serie 1 und 2) als auch im Feld als äußerst beliebt erwies, ist *Brassica napus* (Blätter). Außer den in den Blättern enthaltenen Proteinen und Carotinoiden mit Vitamin-A-Wirkung (Hänsel et al. 1971–1979, 1992–1994) sind keine Inhaltsstoffe der Blätter dieser Pflanze bekannt, die für diese hohe Attraktivität verantwortlich sein könnten. Das Fehlen von Glucosinolat und Erucasäure im 00-Raps ist mit großer Wahrscheinlichkeit nicht ausschlaggebend, da bereits Stein (1958) über die Beliebtheit von Winterraps berichtete, als 00-Raps noch nicht angebaut wurde. Folgende Angaben über Inhaltsstoffe einiger der getesteten Pflanzen könnten eventuell deren Unbeliebtheit erklären:

Die Blätter von *Oenothera biennis*, die in Serie 1 kaum angerührt wurden, enthalten Quercetin (ein Flavonoid) sowie 11% Gerbstoffe (Hänsel et al. 1992–1994). Am bekanntesten unter den Gerbstoffen ist Tannin, das bei einer Konzentration über 2% Säugetiere vom Fressen abhält (Swain 1979). Die Wurzel von *Pastinaca sativa* enthält Pastinacin (ein Alkaloid) und Furanocumarine (Hänsel et al. 1971–1979, 1992–1994). *Leucanthemum vulgare* ist schwach cyanogen und enthält Polyacetylene und Flavonoide (Hegnauer 1962–1986; Hänsel et al. 1992–1994). In *Verbascum densiflorum* sind Flavonoide vorhanden (Krneta-Jordi 1998).

Danksagungen

D. Pavelic und E. Vogel danken wir für die Hilfsbereitschaft bei der Bestimmung der Kohlenhydrate bzw. Phenole. H. J. Bachmann sind wir für die Durchführung der Stickstoffanalyse dankbar. M. Gygli stellte seine Felder als Untersuchungsgebiet und J.-P. Charles die Makrolonkäfige zur Verfügung. E. Hashorva und D. Dietrich danken wir für die statistische Beratung und T. Frank sowie F. Balmelli für die kritische Revision des Manuskripts.

Zusammenfassung

Die Nahrungswahl der Feldmaus *Microtus arvalis* bezüglich Pflanzen der Agrarlandschaft wurde mittels Futterwahlexperimenten im Labor untersucht. Als qualitativer Vergleich diente die Untersuchung der Fraßspuren im Feld. Mit der Bestimmung einiger Pflanzeninhaltsstoffe (Stickstoff, Zucker, Stärke und Phenole) sowie des Energie- und Wassergehalts wurde nach einer Ursache der Präferenzen gesucht. Aus den Wahlversuchen stellte sich eine stark ausgeprägte Selektivität bei der Nahrungswahl heraus. Sehr beliebte Pflanzen waren unter den Kulturpflanzen *Hordeum vulgare* (Blätter), *Brassica napus* (Blätter) und *Beta vulgaris altissima* (Rübe) bzw. unter den Buntbrachepflanzen *Achillea millefolium* (Blätter) und *Trifolium pratense* (Blätter). Zwischen den Präferenzen und den analysierten Nahrungskomponenten bestand keine Beziehung. Von den fünf im Labor sehr attraktiven Pflanzen wurden im Feld nur an *T. pratense* und *B. napus* oft bzw. sehr oft Fraßzeichen beobachtet.

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Z. Säugetierkunde **64** (1999) 169–175

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Parental care and time sharing in the Mongolian gerbil

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Receipt of Ms. 02. 10. 1998
Acceptance of Ms. 14. 01. 1999

Abstract

The biparental care behaviour of the social Mongolian gerbil (*Meriones unguiculatus*) was quantified from birth to weaning of the young under laboratory conditions. Nestbuilding, nest-residence, and retrieving of the offspring were measured. The behaviour of the parents was registered per video-observation on days 2, 5, 8, 13, and 20 after the birth of the young, each for 24 h. To obtain control data, we additionally observed all pairs for 24 h without progeny. The objective of our study was to evaluate the paternal and maternal efforts in rearing the young and to focus on parental time sharing in the nest.

The female made the greatest contribution to care since there was no paternal support in building of the litter-nest and retrieving of the young. However, both adults cooperated via their synchronized presence with the young (temporal coordination or time sharing in the nest). We suggest that via this mutual behavioural synchronization the physiological strains of the female caused, e. g., by lactational hyperthermia are reduced.

Key words: *Meriones unguiculatus*, parental care, time sharing

Introduction

Although in mammals the females mainly care for the young, paternal investment can also increase their chances of survival via direct support, such as warming, and more indirect assistance like nest-building or defending the young. Investigations on cooperative breeding and paternal care mainly refers to primates and carnivores (for a review see: Solomon and French 1997; for rodents: Ostermeyer and Elwood 1984; Solomon and Getz 1997; Gerlach 1998).

Based on short-term observations during the light period (90 minutes per family), Elwood (1979) showed that certain parental activities of the social Mongolian gerbils, e. g., nest-building, are influenced by the other parent. The aim of our long-term study was to quantify in greater detail paternal and maternal efforts from birth to weaning of the altricial young and to focus on parental time sharing in the nest.

Material and methods

Animals and housing

We selected six adult males and six females from a laboratory colony of Mongolian gerbils (*Meriones unguiculatus*). The animals came from different litters and were caged in pairs after weaning at 6–8 weeks. They were kept in climatised rooms with a photoperiod of 12:12 h light (200–300 lx per

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cage): dark (5–10 lx per cage) (light period: 0700–1900 h Central European Time). The room temperature was 24 ± 2 °C and the relative humidity varied from 65–70 %. The cages (size: 55 × 33 × 20 cm) were plastic with a wire mesh top and included a circular treadmill (30 cm in diameter and a running wheel area width of 10 cm). Water and food pellets (Altromin® 7024, Altromin GmbH, Lage) were provided ad libitum. The animal bedding was provided from Altromin GmbH, Lage. To facilitate nest-building, the animals were also provided with cellulose.

We confirm that the experiments have been performed in accordance with local animal welfare legislation and the legal requirements of Germany.

Data analysis and statistics

The parental care behaviour of five pairs towards their first litter and of one pair towards their third litter was observed over 1 600 h. The mean litter size was 5.1 pups (3–7). The behaviour of the parents was registered on days 2, 5, 8, 13, and 20 after the birth of the young (day of birth = day 0), each for 24 h. To obtain control data, we observed all pairs for 24 h without offspring, i. e., 2–3 weeks before birth or after weaning. We used the time-lapse videotechnic (Panasonic WV-CL352E u. AG-7350) and chose the 12 h mode. The analysis was performed using the software The Observer V 3.0 (Noldus, NL). For both pair partners we collected the following behaviours: nest-building (duration): time spent with the carrying-in and arranging of nesting material; nest-residence (duration): time spent in the nest; retrieving of the young (frequency): carrying the pups back to the nest. The parameters are given as mean values, the statistical measure of variance is the standard error. The Friedman analysis of variance and subsequently the two-tailed Wilcoxon test were used to assess the differences of the means. Differences were significant at $p < 0.05$ (* in the graphs). The computer package used for the statistical analyses was Winstat (V 3.1).

Results

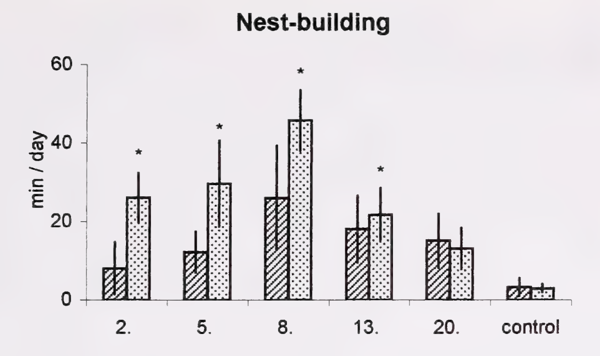
Nest-building

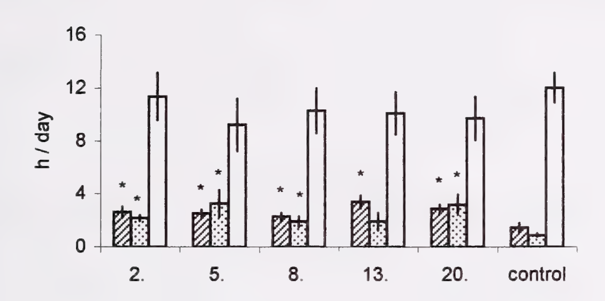
The time the gerbils spent on nest-building depended on whether it was used as a nest for resting (rest-nest) or as a nest for the approaching litter (litter-nest), i. e., the nest had two functions. When the adults lived without young under laboratory conditions, both males and females built a rest-nest as a depression in the animal bedding which was located in a corner of the cage (Fig. 1, males vs. females: Wilcoxon test, $z = -0.94$, $N = 6$, $p > 0.05$). It was only slightly enlarged during the last activity period before and completed just after birth of the pups. This litter-nest was more compact and was also built by both sexes.

Nevertheless, regarding the whole observation period, the respective effort of male and female was different (Fig. 1). In the mean a male invested 15.9 ± 7.4 and a female 27.3 ± 4.7 minutes per day (males vs. females: Wilcoxon test, $z = -1.99$, $N = 6$, $p < 0.05$). Whereas males did not intensify the nest-building behaviour (day 2–day 20 vs. control: Friedman ANOVA, chi-square approximation, $\chi^2 = 8.3$, $N = 6$, $df = 5$, $p > 0.05$), it was significantly elevated in the females until day 13 (day 2–day 20 vs. control: Friedman ANOVA, chi-square approximation, $\chi^2 = 15.64$, $N = 6$, $df = 5$, $p < 0.05$; Wilcoxon test, day 2 vs. control: $z = -1.99$, $N = 6$, $p < 0.05$; day 5 vs. control: $z = -1.99$, $N = 6$, $p < 0.05$; day 8 vs. control: $z = -2.2$, $N = 6$, $p < 0.05$; day 13 vs. control: $z = -1.99$, $N = 6$, $p < 0.05$; day 20 vs. control: $z = -1.36$, $N = 6$, $p > 0.05$).

Nest-residence

Both males and females stayed for approximately the same time alone in the commonly established nest (Fig. 1). There were no intersexual differences in that respect either in the rest-nest (Wilcoxon test, $z = -1.36$, $N = 6$, $p > 0.05$) or in the litter-nest (Wilcoxon test, $z = -0.52$, $N = 6$, $p > 0.05$). In the presence of the young this separate nest-residence of the





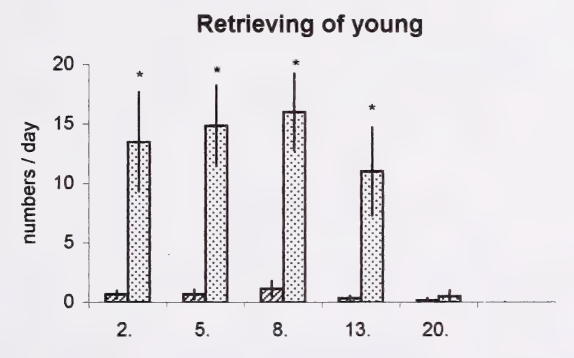


Fig. 1. Biparental care in Mongolian gerbils. Data of six pairs. Day 2 to day 20: with young (day 0 = day of birth); control: without young; scattered columns = males; dotted columns = females; blank columns = both parents together; bars = standard error of mean. * $p < 0.05$; The Friedman analysis of variance and subsequently the two-tailed Wilcoxon test were used to assess the differences of the means (for details, see text).

adults increased, i. e., the two parents showed time sharing in the litter-nest. This increase of the sole care for the progeny was always significant for the males (day 2–day 20 vs. control: Friedman ANOVA, chi-square approximation, $\chi^2 = 13.38$, $N = 6$, $df = 5$, $p < 0.05$; Wilcoxon test, day 2 vs. control: $z = -1.99$, $N = 6$, $p < 0.05$; day 5 vs. control: $z = -1.99$, $N = 6$, $p < 0.05$; day 8 vs. control: $z = -2.2$, $N = 6$, $p < 0.05$; day 13 vs. control: $z = -2.2$, $N = 6$, $p < 0.05$; day 20 vs. control: $z = -1.99$, $N = 6$, $p < 0.05$). The same applies to the females ex-

cept for day 13 (day 2–day 20 vs. control: Friedman ANOVA, chi-square approximation, $\chi^2 = 17.4$, N = 6, df = 5, $p < 0.05$; Wilcoxon test, day 2 vs. control: z = –2.2, N = 6, $p < 0.05$; day 5 vs. control: z = –2.2, N = 6, $p<0.05$; day 8 vs. control: z = –2.2, N = 6, $p < 0.05$; day 13 vs. control: z = –1.4, N = 6, $p > 0.05$; day 20 vs. control: z = –2.2, N = 6, $p < 0.05$).

The common nest-residence, i. e., the time the adults spent together in the nest as a pair, was about four times longer than the separate stay (Fig. 1). However, in contrast to this, it was not affected by the offspring (day 2–day 20 vs. control: Friedman ANOVA, chi-square approximation, $\chi^2 = 11.5$, N = 6, df = 5, $p < 0.05$; Wilcoxon test, day 2 vs. control: z = –0.94, N = 6, $p > 0.05$; day 5 vs. control: z = –1.57, N = 6, $p > 0.05$; day 8 vs. control: z = –1.36, N = 6, $p > 0.05$; day 13 vs. control: z = –1.57, N = 6, $p > 0.05$; day 20 vs. control: z = –1.78, N = 6, $p > 0.05$).

Summing up the data of the separate and the paired nest-residence results in the total time the adult gerbils spent in the nest. It ranged from 14.4 ± 1.2 h per day (control) and 15.4 ± 1.8 h per day (mean of day 2–day 20). As for the common nest-residence, the statistical analysis showed that there was no difference between these two periods (day 2–day 20 vs. control: Friedman ANOVA chi-square approximation, $\chi^2 = 11.98$, N = 6, df = 5, $p < 0.05$; Wilcoxon test, day 2 vs. control: z = –1.21, N = 6, $p > 0.05$; day 5 vs. control: z = –0.52, N = 6, $p > 0.05$; day 8 vs. control: z = –0.37, N = 6, $p > 0.05$; day 13 vs. control: z = –1.36, N = 6, $p > 0.05$; day 20 vs. control: z = –1.36, N = 6, $p > 0.05$).

Retrieving of young

Until day 5, the progeny were passively dragged out of the nest while attached to the mothers nipples. Nevertheless, to an even greater extent they were thrown out of the nest by digging movements of the adults. With advancing age and increased locomotor activity the pups actively left the nest and were retrieved essentially by females (Fig. 1, males vs. females: Wilcoxon test, day 2: z = –2.2, N = 6, $p < 0.05$; day 5: z = –2.2, N = 6, $p < 0.05$; day 8: z = –2.2, N = 6, $p < 0.05$; day 13: z = –2.2, N = 6, $p < 0.05$; day 20: z = –0.48, N = 6, $p > 0.05$). The mothers grabbed the young in the neck or other parts of the body with their teeth. At day 20 the retrieving behaviour of females ended.

The males also tried to retrieve their offspring but they pushed the young back to the nest with their snout. However, they failed in all observed cases.

Discussion

In nature Mongolian gerbils live under territorial conditions in groups which are established by a founder pair (BANNIKOV 1954; AGREN 1984; HENDRIE and STARKEY 1998). In addition to the female, the male and the other family members also participate in promoting the development of the offspring (ELWOOD 1975; OSTERMEYER and ELWOOD 1984). During their first days they have an incompleted ability to thermoregulate and are warmed and sheltered in a nest by the parents in order to stay alive. Paternal behaviour is described also in other rodent species. WOLFF and CICIRELLO (1991) showed that *Peromyscus maniculatus* males retrieved pups and nested with females and newborn pups. In the laboratory adult gerbils built plain nests for common resting (rest-nest). For rearing the altricial young, the nests were enlarged and constructed more compactly mainly by the females (litter-nest). As shown in the golden hamster, the size of the nest and the amount of the female nest-building activity do not depend on the sexual cycle or the state of gravidity but on the environmental temperature (RICHARDS 1966; BHATIA et al. 1995). Since the room temperature in our experiments was high (23–25 °C), the nest-building activity was relatively low. The increase in the female nest-building behaviour immediately after the birth of the pups is a response to parturition and the presence of

the young. Besides the temperature, the nest-building behaviour in house mice and other myomorph rodents is intensified according to olfactorical and acoustical (ultrasonic-) stimuli of the young (Noirot 1972, 1974; Sales and Smith 1978). Two weeks after birth the coat of the pups is well developed and the reduced relative surface of the body diminishes the loss of body heat. This shift of the young gerbils from being "heat sinks" to "heat sources" is reflected in a reduction of the nest-building effort following day 13.

In contrast to the female-biased nest-building both males and females cared for the progeny in the nest. While one animal stayed in it and warmed the young, the other left it. This ensues from the increased separate nest-residence of the father and the mother after the litter, i. e., there was an intersexual time sharing in the nest. Even in the prairie vole, *Microtus ochrogaster*, the female does leave the nest more often when the male takes part in the care of the litter (Wang and Novak 1992). Nevertheless, in this case the data were not calculated for timed synchrony. Wynne-Edwards (1995) observed the care behaviour of *Phodopus campbelli* for 30 minutes per day during the activity phase and during rest, respectively. She was also able to prove a temporal synchronisation in the care behaviour between the parents and additionally between mother and sister, i. e., the aunt of the offspring. The cooling down of the pups is prevented due to this temporal coordination of parental behaviour. Furthermore, the mother is able to satisfy her increased need for nutrients following the litter and during lactation (Galef 1983) and to reduce the physical strain caused by the lactational hyperthermia. This phenomenon of an increased core body temperature while in physical contact with the young is described in various small mammals (Adels and Leon 1986; Scribner and Wynne-Edwards 1994 a, 1994 b). In gerbils the daily mean values of core body temperature during the whole period of lactation are elevated by 0.6 °C (Weinandy and Gattermann 1995).

Although the common nest-residence of the pair partners was longer than the separate ones, it was not influenced by the pups. In accordance to their nocturnal activity pattern (Weinandy and Gattermann 1996/97) and their social behaviour gerbils rest together during most of the light phase, irrespective of the presence of young. They were left alone in the nest for about 8.6 h per day, i. e., the pups were not constantly warmed by the parents. Our assumption is that this is a consequence of the relatively high temperature conditions in the laboratory. Furthermore, the mutual warming of the young also reduced the loss of heat.

Retrieving the offspring is another direct nursing effort, which was in our study only successfully carried out by the female. The observed increase of retrieval behaviour was most likely triggered by ultrasonic vocalisation and the growing locomotor activity of the young, which left the nest more frequently. Furthermore, they were thrown out of the nest due to the species-specific stereotypic digging behaviour of both adults (Wiedenmayer 1997). Nevertheless during the rearing period, the females tended to dig more often (67 to 88 minutes per day; unpubl. obs.). Similar results for this species were obtained by Kaplan and Hyland (1972) and they considered this phenomenon an indication of female hyperactivity connected with litter and lactation.

In conclusion, in gerbils there is no paternal support in the building of the litter-nest and the retrieving of the young. Both adults cooperate via their synchronised presence with the young (temporal coordination or time sharing in the nest). We suggest that via this mutual behavioural synchronisation the physiological strains of the female caused by lactational hyperthermia are reduced.

Acknowledgements

We thank Anja Sonntag and Steffen Wachs for technical assistance and Kate Williams for correcting the English. The work was supported by the DFG (Ga 434/1–2).

Zusammenfassung

Elterliche Jungenpflege und zeitliche Kooperation bei der Mongolischen Wüstenrennmaus

Das elterliche Pflegeverhalten der sozial lebenden Mongolischen Wüstenrennmaus (*Meriones unguiculatus*) wurde von der Geburt bis zur Entwöhnung der Jungen unter Laborbedingungen quantitativ erfaßt. Nestbau, Nestaufenthalt und das Eintragen der Jungtiere wurden analysiert. Die Registrierung dieser Verhaltensweisen der Elterntiere erfolgte per Videobeobachtung an den Tagen 2, 5, 8, 13 und 20 nach der Geburt der Jungen (Tag der Geburt = Tag 0) für jeweils 24 Stunden. Als Kontrolle wurden alle Paare darüber hinaus einmalig für 24 Stunden ohne Nachwuchs beobachtet. Neugeborene Mongolische Wüstenrennmäuse sind typische Nesthocker. Ziel dieser Studie war es, den väterlichen und den mütterlichen Aufwand bei der Jungenaufzucht zu ermitteln. Das Weibchen leistete insgesamt den größten Anteil an der Jungenpflege, da es keine männliche Unterstützung beim Bau des Wurfnestes oder beim Eintragen der Jungtiere gab. Dagegen kooperierten beide Elterntiere aufgrund ihrer synchronisierten Anwesenheit bei den Nestlingen miteinander (temporale Koordination). Wir vermuten, daß durch diese wechselseitige Verhaltenssynchronisation die physiologischen Belastungen des Muttertieres, beispielsweise verursacht durch die Laktationshyperthermie, reduziert werden können.

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Effects of sex and breeding status on habitat selection by feral House mice (*Mus musculus*) on a small Mediterranean island

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Receipt of Ms. 03. 04. 1998
Acceptance of Ms. 16. 02. 1999

Abstract

Patterns of habitat use of the house mouse (*Mus musculus*) in relation to sex and breeding status were studied in April and May (the early breeding season) in two structurally different habitats on a small Mediterranean island in NE Spain. Overall mice abundance increased from bare and rocky areas to areas with a dense cover of shrubs and herbaceous plants. Females were associated to shrub areas in April, shifting towards more herbaceous areas in May. Males were less selective, being only slightly related to shrub height in April, and they were not associated with structural habitat features in May. Overlap in habitat use by sexes existed in both months, being more reduced in April than in May.

Female densities were significantly higher in the habitat with dense vegetation cover (suitable habitat) than in the habitat with scarce vegetation in both months, while densities of males were not. Male density decreased from April to May in the suitable habitat, and intersexual competition was exclusively detected in the period of higher male density. In this habitat, intraspecific competition explained the spatial distribution of sexes regardless of habitat structure characteristics. In absence of competition the spatial distribution of sexes was mainly related to habitat structure.

Females and males started sexual activity early in the season in the suitable habitat. Weight of females was higher in suitable habitat in both months, also showing a positive association with the herbaceous cover, and the average weights of males and females at trapping stations were positively associated.

Our results are finally discussed in relation to the social organisation models proposed for house mouse populations.

Key words: *Mus musculus*, island, habitat selection, sex, breeding status

Introduction

The house mouse is a widespread species, living in mainland Europe as well as on Mediterranean islands (Orsini et al. 1983; Amori et al. 1984). Northern populations are mainly comensal to human settlements but live outdoors for a great part of the year (Carlsen 1993). In Southern Europe, however, feral populations are found throughout the year, e. g. in Mediterranean habitats (Cassaing and Croset 1985; Cagnin et al. 1996). Also Iberian populations are mainly linked to human dwellings (Sans-Coma et al. 1987; Gosàlbez 1987) but some local and well-established feral populations are present in moist habitats (Gosàlbez 1987). Some differences in habitat selection are related to interspecific competition, of which this species seems especially sensitive (Boitani et al.

0044-3468/99/64/03 – 176 $ 12.00/0

1985; FAIRLEY and SMAL 1987). Additionally, its distribution is conditioned in insular habitats by competition with other rodent species rather than by habitat structure (DUESER and PORTER 1986).

Mammal communities on islands differ in some ecological aspects from those on the mainland (BLONDEL 1986). These differences are mainly related to the degree of isolation, which is a problem to the colonisation of non-volant mammals from the mainland. They are also related to the surface and the size of the island, where small areas are not to be colonized by medium- or large-sized mammals, i. e., carnivores (BLONDEL 1986). As a consequence, smaller islands normally are poor in species, and small mammal communities living on islands have special features of habitat use because of reduced predation pressure and interspecific competition (CROWELL 1983).

In this study we investigated the physical cues that may influence habitat use of a feral house mouse population on a small archipelago uninhabited both by humans and also by other rodents. Our objectives are to analyse spatial distribution of the species at a certain time in relation to habitat structure, sex, and breeding status, and to provide some information on the social organisation of house mice in insular habitats.

Material and methods

The study was performed on the Medes Islands (42°0′N, 3°13′E, NE Spain) during spring 1996. These islands are a small calcareous archipelago only 0.9 km off the coast. The vegetation of the archipelago is dominated by nitrophylous communities linked to the presence of one of the largest breeding colonies of yellow-legged gulls (*Larus cachinnans*) in the Mediterranean (BOSCH et al. 1994). Three main habitats differing in vegetation features are distinguished within the islands: (1) shrubby habitat, dominated by *Atriplex halimus*, a dense shrub which reaches 70–100 cm height; (2) grassy habitat, dominated by grassy, ruderal plants, such as *Hordeum murinum*; and (3) bare habitat, with very scarce vegetation, bare ground and dispersed rocks (see BOSCH and SOL 1998). The archipelago was transitorily occupied by humans until 1923, being deserted for the last 70 years. The small mammal community of these islands is composed of house mice (*Mus musculus*) and white-toothed shrews (*Crocidura russula*) (GOSÀLBEZ et al. 1984).

Two plots of 49 and 25 Sherman live traps (i. e. 7 rows × 7 columns of traps, and 5 rows × 5 columns of traps, respectively, equidistance between traps 16.6 m) were set during three consecutive days from 31 March to 2 April (first session), and from 26 to 28 May (second session) on the largest island of the archipelago (Meda Gran, 18.2 ha). The study was conducted during the early breeding season of the house mouse which is described to last from spring to late summer on the Medes islands (GOSÀLBEZ et al. 1984). Traps were baited with a mixture of tuna fish in olive oil and flour to allow increasing trappability, since low trappability might explain low recapture rates (KREBS et al. 1994). Trapping effort for each trapping session was 222 trapnights/session. The large plot was 1 ha in area and included the shrubby and grassy habitats, while the small one was 0.5 ha and only included the bare habitat.

The trapping plots were examined early in the morning and the animals found were identified, weighed, sexed, examined for reproductive condition and marked by toe-clipping (GURNELL and FLOWERDEW 1990), and released at the trap station. To allow comparisons between plots and months, population densities were estimated as the average number of individuals caught per trapping station during the three consecutive days.

The habitat structure was characterized at each trap station at the same time when trapping was conducted, by means of estimating values of height and cover on a 5 m radius circular plot centred around the Sherman trap (ALCÁNTARA and TELLERÍA 1991).

Two factorial analyses (BHATTACHARYYA 1981) were performed (one per month) with the habitat structure variables of all traps to obtain independent multivariate factors considered as gradients to which the frequencies of occurrence of the small mammals refer.

To ascertain preferences of the house mouse spatial distribution, the frequency of captures at each trap station was considered as a relative measure of density in the surrounding habitat (DUESER and HALLETT 1980), and then was related to the habitat structure variables by means of non-para-

metric Spearman correlation analysis. To test for intersexual competition and its influence on habitat use, we used the method described by Hallett and Pimm (1979). The unweighed average situations of the sexes on the factorial space were obtained by averaging the values of the factor scores of the trapping stations with captures on the factors extracted. To ascertain the habitat variables that best explained the abundance of the house mice, stepwise multiple regression analysis was performed, with the frequencies of occurrence as dependent variables and the habitat variables as the independent ones (Yahner 1982). To avoid autocorrelation in habitat variables, multiple regression analyses were also performed with factors as the independent variables, and the Bonferroni correction was applied when necessary to maintain $\alpha < 0.05$ (Rice 1989).

Microhabitat characterization of the house mouse feral population was estimated as the average values of the habitat variables at the trap stations where the species or sexes were trapped (selected areas). These values were compared with the average values of the habitat variables at the trap stations where the species or sexes were not trapped (non selected areas), using the Kruskal-Wallis ANOVA. When possible, these tests were also used to verify sexual and temporal habitat preferences. Mann-Whitney U-tests were performed to ascertain differences in habitat preferences between sexes, and for the same sex between different trapping sessions. To simplify the statistical analysis, overlap in habitat use by sexes was estimated as the z-value obtained when testing for differences between average values of both sexes on each of the multivariate factors extracted (using Mann Whitney U-test). The greater the z-value the smaller is the overlap.

Possible differences in the relative abundances of house mice between plots, months or sexes were tested by Chi-square analysis (with the Yates' correction for continuity) on standardized trapping areas.

The differences between the two sampling periods in habitat structure as well as in house mouse variables at the same trapping stations were tested with the Wilcoxon signed-rank test for matched pairs. Before parametric statistical treatment, variables were log (x + 1) and arcsine transformed (Zar 1996).

Results

Habitat structure

The two habitats sampled were structurally different in both periods (Tab. 1). Plot 1 was characterized by higher values of vegetation cover, and plot 2 by higher values for the slope and rock cover. Monthly variation of habitat structure was only observed in the herbaceous cover and height.

The factorial analysis performed with the structural variables yielded similar results in both periods. In April, two eigenvectors were extracted, explaining altogether 75.5% of the structural habitat variance (Tab. 2). The first factor was positively correlated to the rock and dead vegetation cover and to the slope. It was negatively related to shrub and herbaceous cover, and height of shrubs and herbaceous plants. This factor was interpreted as the negative effects of the increasing slope on the establishment of vegetation strata. The second factor was positively related to shrub cover, shrub height, and slope, but negatively related to herbaceous height. Since shrub cover and height had positive loadings, and herbaceous cover had a negative loading, this factor was interpreted as a negative effect of the shrub plants on the development of the herbaceous plants. The factorial analysis conducted in May yielded similar results (Tab. 2).

House mouse abundance in relation to sex and breeding status

61 individuals of *Mus musculus* (37 males, 24 females) were trapped in April, and 46 individuals (22 males, 24 females) were trapped in May (Tab. 3).

The relative abundance of *M. musculus* was greater in plot 1 than in plot 2 for both periods (April: $\chi^2 = 7.88$, $p < 0.01$, d. f. = 1; May: $\chi^2 = 7.54$, $p < 0.01$, d. f. = 1). Male density decreased from April to May ($\chi^2 = 3.90$, $p < 0.05$, d. f. = 1), while female density remained

Table 1. Structural variables (mean ± standard error) measured at trapping stations in plots one and two in both periods (April and May), and average and s. e. values for the house mouse densities and weights. Differences between plots tested with Mann Whitney U-tests, and differences between sampling periods with Wilcoxon tests (level of significance: * (p < 0.05), ** (p < 0.01), *** (p < 0.001), **** (p < 0.0001)).

Variable	April			May			Differences April–May	
	Plot 1 (n = 49)	Plot 2 (n = 25)	U-test z and p	Plot 1 (n = 49)	Plot 2 (n = 25)	U-test z and p	Plot 1 z and p	Plot 2 z and p
Slope (%)	4.28 ± 0.96	15.2 ± 1.96	4.94****	4.28 ± 0.96	15.2 ± 1.96	5.41****	0	0
Rock cover (%)	7.95 ± 1.36	42.08 ± 4.46	5.84****	7.95 ± 1.36	42.0 ± 3.82	6.34****	0	0.92
Shrub cover (%)	25.2 ± 3.9	0.41 ± 0.28	4.78****	26.02 ± 3.74	0.16 ± 0.11	4.90****	0.89	1.78
Height of shrubs (cm)	77.58 ± 8.35	5.35 ± 4.28	4.71****	77.60 ± 7.93	5.60 ± 3.91	4.90****	0.25	1.78
Herbaceous cover (%)	66.92 ± 3.22	4.0 ± 1.62	6.82****	59.59 ± 2.50	37.60 ± 3.61	4.23****	3.40***	4.30****
Herbaceous height (cm)	37.48 ± 1.99	3.90 ± 1.81	6.50****	82.32 ± 2.99	24.59 ± 3.54	6.88****	6.09****	3.95***
Dead vegetation (%)	9.92 ± 1.12	32.08 ± 3.37	5.52****	21.74 ± 1.44	14.20 ± 2.57	3.12**	4.48****	3.53***
Density								
females	0.42 ± 0.10	0.12 ± 0.06	1.74	0.53 ± 0.10	0.16 ± 0.09	2.34**	0.80	0.13
males	0.67 ± 0.12	0.40 ± 0.11	0.97	0.32 ± 0.07	0.40 ± 0.14	0.03	2.30*	0.08
total	1.14 ± 0.16	0.52 ± 0.14	2.19*	0.85 ± 0.14	0.56 ± 0.19	1.33	1.47	0.40
Body weight (g)								
females	17.60 ± 0.57	12.0 ± 1.0	2.51**	20.05 ± 1.15	13.5 ± 1.32	1.90*	2.31*	1.61
males	15.78 ± 0.42	15.33 ± 0.95	0.13	17.0 ± 0.84	16.89 ± 0.74	0.10	0.81	0.70
total	16.35 ± 0.35	15.00 ± 0.81	1.40	18.89 ± 0.69	16.00 ± 1.09	1.97*	3.23**	0.62

Table 2. Factorial analysis performed with the habitat structure variables in both months, and level of significance of the correlations between variables and factors (see Tab. 1).

Variable	April		May	
	Factor 1	Factor 2	Factor 1	Factor 2
Slope	0.68****	0.45****	0.69****	0.30**
Rock cover	0.78****	0.14	0.85****	0.07
Shrub cover	–0.63****	0.71****	–0.62****	0.75****
Shrub height	–0.73****	0.58****	–0.68****	0.63****
Herbaceous cover	–0.83****	–0.43***	–0.56****	–0.70****
Herbaceous height	–0.88****	–0.09	–0.88****	–0.14
Dead vegetation cover	0.70****	0.09	–0.49****	–0.19
Eigenvalue	4.00	1.28	3.42	1.62
% Variance	57.2	18.3	48.9	23.1
Ac. % Variance	57.2	75.5	48.9	72.1

Table 3. Number of house mouse individuals trapped in relation to sex (n), frequency of recapture (FR) within the same sampling period and breeding status (BS: frequencies of active males with scrotal testes and pregnant females) in the two plots (P1 and P2) and sampling periods (April and May).

	April						May					
	P1			P2			P1			P2		
	n	FR	BS	n	FR	BS	n	FR	BS	n	FR	BS
males	28	17.8	65.3	9	11.1	33.3	16	6.2	47.6	6	66.6	83.3
females	20	14.2	28.5	4	0	0	20	30	80.9	4	0	25

Table 4. Spearman non-parametric correlation matrix between house mouse relative abundances and habitat structural variables in both months (significance levels as in Tab. 1). F1 = Factor 1; F2 = Factor 2; Rc = Rock cover; Sc = Shrub cover; Sh = Shrub height; Hh = Herbaceous height; only significant correlations ($p < 0.007$, Bonferroni correction) are shown. Slope, dead vegetation, and herbaceous cover with no significant correlations. Levels of significance as in Tab. 1.

Group	Month	F1	F2	Rc	Sc	Sh	Hh
females	April	–0.30**	0.36***	–0.31**	0.44***	0.32**	
	May	–0.29**					0.35**
males	April					0.05*	
	May						
total	April	–0.37***	0.45****		0.46****	0.41***	0.36**
	May						
total	April + May	–0.35**	0.39***		0.48****	0.37***	0.36**

the same ($\xi^2 = 0.01$, $p > 0.05$, d.f. = 1). Considering the captures on both plots, the sex-ratio was biased towards males in April (males : females, 1.7 : 1; $\xi^2 = 4.42$, $p < 0.05$, d.f. = 1), but not in May (males : females 1.1 : 1; $\xi^2 = 2.7$, $p > 0.05$, d.f. = 1).

Both males and females attained sexual activity earlier in plot 1 (Tab. 3). Later the number of active males decreased at the same time when females become pregnant. In plot 2, females could be considered transient since no recaptures were obtained. Sexually active males increased later in plot 2, and the high recapture rate obtained might be considered as a degree of site-attachment.

General patterns of abundance in relation to habitat structure

M. musculus showed clear patterns of relative abundance in relation to habitat structure in April, but a more vague pattern in May (Tabs. 4 and 5). The habitat structure variables that explained most of the presence of the species were the height of shrubs in April and the herbaceous height in May. Pooling capture data from both months, *M. musculus* showed significant preferences for traps with higher values for height and cover of shrubs ($r_s = 0.90$ and $r_s = 0.88$, respectively, $n = 7$, $p < 0.05$; Fig. 1).

Table 5. Results of the stepwise multiple regression analysis performed with the habitat structure variables or factors as independent variables, and house mouse relative abundance as dependent variables, showing the first variables selected and the percentage of variance explained by the models. Levels of significance as in Tab. 1.

	April		May		April + May	
Dependent variable	Variable selected	R^2 and p	Variable selected	R2 and p	Variable selected	R^2 and p
males	–	0	–	0	Factor 2	0.06**
	Shrub height	0.05*	–	0	Shrub cover	0.05*
females	Factor 1	0.17****	Factor 1	0.06**	Factor 1	0.22****
	Shrub cover	0.18****	Herbaceous height	0.07**	Shrub cover	0.23****
total	Factor 2	0.23****	–	0	Factor 1	0.21****
	Shrub height	0.22****	Herbaceous height	0.06**	Shrub height	0.23****

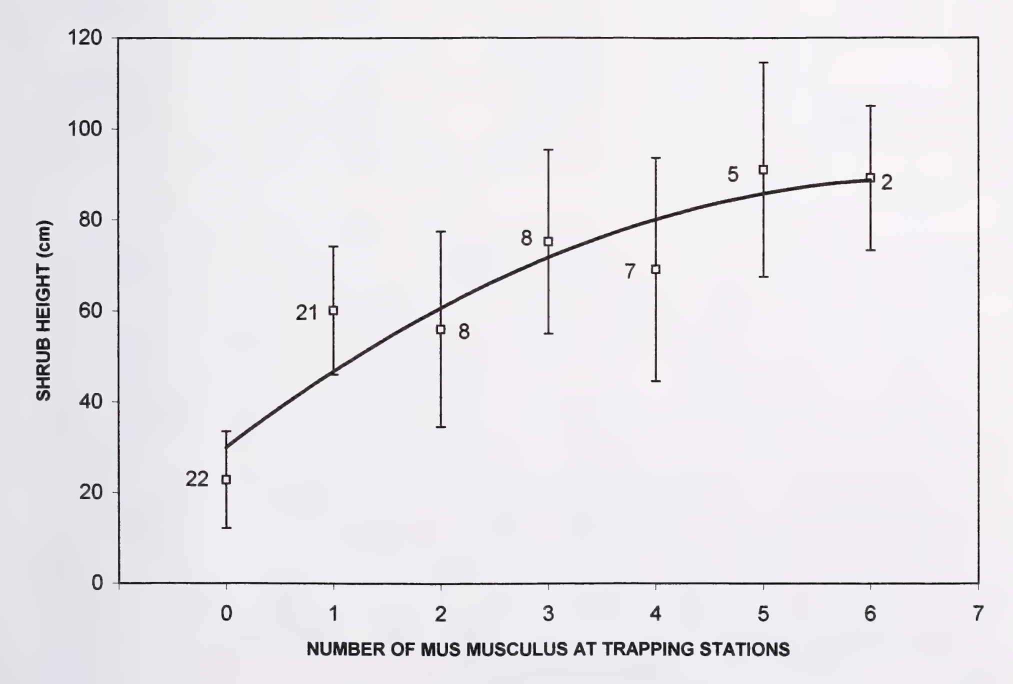


Fig. 1. Frequencies of capture of *Mus musculus* at trapping stations in relation to average (± standard error) of shrub height. Numbers are sample sizes for each category.

Microhabitat preferences in relation to sex and month

A) April: Females showed marked microhabitat preferences, while males did not. Females showed significant correlations with both factors; their abundance increased along factor 2 and decreased along factor 1 (Tab. 4), meaning that areas with higher vegetation cover and height were selected and rock covered areas were avoided. The shrub cover explained the greater amount of variance (19%) in female correlations with the structural variables, followed by height of shrubs (10%), rock cover (9%) and herbaceous height (8%). Males did not show any correlation with both factors and only one correlation with the structural variables (Tabs. 4 and 5). Habitat used by both sexes overlapped in both factors (values for overlap on F1 and F2 were 0.91 and 1.18, respectively), but females were more selective. Furthermore, the centroids of males and females on both factors differed significantly from the centroids of the non-capture sites (Tab. 6), suggesting the avoidance of a part of the habitat available. The distance of the factorial space defined by factors 1 and 2 from male to female centroids was 0.46.

Table 6. Situation (average ± standard error) of *Mus musculus* (males, females and both sexes pooled) on the structural factors extracted by the factorial analyses performed in both months, and average situation of non-capture sites. Asteriscs show significant differences between mean values of the species or sexes and the non-capture values on both factors (differences tested with U-Mann-Whitney tests, and level of significance as in Tab. 1).

Variables	April		May	
	Factor 1	Factor 2	Factor 1	Factor 2
males	–0.16 ± 0.18* (n = 31)	0.22 ± 0.18*** (n = 31)	–0.10 ± 0.20 (n = 22)	0.34 ± 0.18 (n = 22)
females	–0.49 ± 0.17** (n = 18)	0.56 ± 0.21**** (n = 18)	–0.42 ± 0.16** (n = 22)	0.12 ± 0.24 (n = 22)
total	–0.25 ± 0.15** (n = 40)	0.29 ± 0.15**** (n = 40)	–0.21 ± 0.14* (n = 32)	0.06 ± 0.17 (n = 32)
Non-capture sites	0.34 ± 0.16 (n = 32)	–0.41 ± 0.15 (n = 32)	0.25 ± 0.17 (n = 38)	–0.19 ± 0.15 (n = 38)

The average weight of females was higher in plot 1 (Tab. 1), and was positively correlated to the herbaceous cover ($r_s = 0.52$, $n = 18$, $p < 0.05$). Thus, heavier females were found on areas with higher herbaceous cover. The average weight of males did not show any relation with the habitat structure variables. Otherwise, a significant and positive correlation was found between the average weight of both sexes at trapping stations ($r_s = 0.69$, $n = 10$, $p < 0.05$).

B) May: The variance explained by the stepwise regression models performed in May with the house mouse relative abundances and the habitat structure variables or factors was derived from the presence of females alone (Tab. 5). On the other hand, the number and significance of correlations between relative abundance and structural variables decreased (Tab. 4). The herbaceous height explained the greater amount of variance in female abundance (12%), followed by rock (7%) and shrub cover (6%). Females correlated negatively with factor 1, but no significant correlation was found with factor 2. Males did not show any correlation with factors or structural variables (Tab. 4). Habitat used by both sexes overlapped in both factors (1.13 on F1 and 0.10 on F2), but the distance on the factorial space defined by factors 1 and 2 from male to female centroids (0.37) was nearly the same as the distance observed in April (0.46). From April to May, habitat used by females shifted along factor two (0.44 units), and slightly along factor 1

(0.07 units). Since factor two is negatively correlated to the herbaceous cover, the increase in female's mean values for this factor can be interpreted as a displacement towards more herbaceous areas. The shift of males was moderate (only 0.13 units for the factorial space).

The average weight of both sexes did not show any relation with the habitat structure variables, but the average weight of females in plot 1 was higher than in plot 2, as occurred in April.

Intersexual competition and habitat use

Negative male-female interactions were detected in April on plot 1, and symmetrical intersexual competition explained the spatial distribution of sexes regardless of habitat structure. In April on plot 2 no male-female interactions were detected, and the spatial distribution of sexes was related mainly to habitat structure characteristics (Tab. 7). The same occurred in May on plot 1, and on plot 2: neither intersexual competition nor habitat structure influenced the spatial distribution of sexes.

Table 7. Multiple regression analysis performed in April and May with the frequencies of occurence of one sex as the dependent variable and both factors extracted and the frequencies of occurence of the other sex as independent variables. The partial regression coefficients, t-values and levels of significance are shown (see Tab. 1).

Month	Plot	Dependent variable	Variables selected	Coefficient	t and p
April	1	Female	Male	–0.48	2.72**
		Male	Female	–0.45	2.72**
April	2	Female	factor 1	–0.60	2.04
		Male	factor 1	0.67	3.74**
			factor 2	0.35	2.69*
May	1	Female	factor 2	0.27	2.19*
		Male	factor 1	0.25	2.30*
May	2	Female	–	–	–
		Male	–	–	–

Discussion

On the Medes Islands the house mouse showed an increasing pattern of its relative abundance from bare and rocky areas to areas covered by shrubby and grassy vegetation. These results are in agreement with the pattern observed in another insular population of *Mus musculus* (Dueser and Porter 1986). *M. musculus* is sensitive to interspecific competition (Fairley and Smal 1987), since its mainland distribution seems to be restricted by the presence of some rodent species which in sympatry exclude *M. musculus* from natural environments (Boitani et al. 1985; Auffray et al. 1990). Insular populations of *M. musculus* are also sensitive to interspecific competition (Dueser and Porter 1986), and the absence of competitors from the Medes Islands could allow *M. musculus* to inhabit natural xeric environments, as reported for feral mainland populations in absence of *M. spretus* (Orsini et al. 1982; Auffray et al. 1990; Cagnin et al. 1996).

The pattern of house mice abundance varied when considering the sampling month, the habitat sampled, and the sex of the individuals trapped. Females density was higher in the plot with higher vegetation cover (suitable habitat). Since females start sexual activity in early spring (Gosàlbez et al. 1984), the higher male density in April might be a

consequence of competition for mating with sexually active females, and the lower density in May as a result of the decreasing number of potential mating partners, with most of the females being pregnant or lactating. Female recapture rates increased as the breeding season progressed on a suitable plot (suggesting a degree of female site-attachment inherent to pregnancy or lactation, Krebs et al. 1994), while male recapture rates decreased at the same time, suggesting a contrary pattern with a greater mobility. The increasing number of active males on the non-suitable plot late in the season could be interpreted as the displacement of active males from suitable to non-suitable habitats in search of sexually active females.

Our results agree with the general pattern of habitat use found in other small mammals, with females selecting microhabitats that provide greater protective cover (Seagle 1985). They tend to shift towards more herbaceous-covered areas as the season progresses (Belk et al. 1988). Males were competing for breeding females (Krebs et al. 1995), and they showed a more reduced habitat selectivity (Belk et al. 1988). This may result from a direct consequence of their greater mobility or from an indirect consequence of their association with females. Different habitat utilisation by sexes seems likely to exist with the consequence to decrease intraspecific competitive pressure on reproductive females (Seagle 1985). Bowers and Smith (1979) documented a case for *Peromyscus maniculatus* in which such a segregation was a result of female dominance over males due to larger body size being a way to maximize reproductive effort. In spite of a general absence of sexual dimorphism concerning body size (Gosàlbez et al. 1984), female house mice were heavier (probably caused by pregnancy) than males throughout the study period on the more suitable plot, and females trapped on this plot were heavier than females trapped on the other plot, regardless time of sampling. The positive relationship between average weight of males and females at trapping stations suggested a hierarchical displacement of subordinates to unfavourable microhabitats by dominant individuals, as has also been reported in laboratory studies (Reimer and Petras 1967).

Finally, the characteristics of the house mouse population studied seems to be in agreement with the social organisation model proposed by Newsome (1969) and supported by Krebs et al. (1995), with feral house mouse populations not being territorial but showing social dominance through body size. Dominant females may aggregate in high resource quality areas, as has been reported for wood mice (Montgomery et al. 1991), and energetic advantages for these females could arise as a result of habitat selection, reducing predation risk (Price and Brown 1983), increasing foraging efficiency (Thompson 1982), or may be living under more favourable microclimatic conditions (Walsberg 1985).

Acknowledgements

We thank A. Arrizabalaga for his technical support and advice throughout the study. J. L. Tella, G. Blanco, J. L. Tellería and two anonymous referees kindly revised the manuscript; A. Villarroya helped with statistics, and M. Zabala, J. M. Serrano, Port Autònom de Barcelona and the Servei de Vigilància de les Illes Medes for their help in the field work.

Zusammenfassung

Auswirkungen von Geschlecht und Fortpflanzungsstatus auf Habitatwahl bei freilebenden Hausmäusen (Mus musculus) auf einer kleinen Mittelmeerinsel

Das Muster der Lebensraumnutzung von freilebenden Hausmäusen (*Mus musculus*) in bezug auf Geschlecht und Fortpflanzungsstatus wurde während des Frühjahrs (April und Mai, d. h. zu Beginn

der Fortpflanzungsperiode) in zwei strukturell verschiedenen Lebensräumen auf einer kleinen Mittelmeerinsel im NE Spaniens untersucht. Im Allgemeinen zeigte die Zunahme in der Abundanz der Hausmaus von felsigen und pflanzenlosen Gebieten zu Bereichen mit einer dichten Deckung durch Sträucher und krautige Pflanzen eine deutliche Bevorzugung bestimmter Habitatstrukturen. Betrachtet man die Geschlechter getrennt, so ergab sich während beider Untersuchungsperioden, daß die Weibchen deutlich wählerischer waren. Eine schrittweise multiple Regressionsanalyse zeigte, daß die Weibchen im April buschartige Gebiete bevorzugten und im Mai zu krautigen Gebieten wechselten. Die Verbreitung der Männchen zeigte im April eine schwache Beziehung zur Höhe der Pflanzen, im Mai war das Vorkommen dagegen weitgehend unabhängig von den Eigenschaften des Lebensraumes. Während beider Monate war in beiden Geschlechtern eine Überlappung in bezug auf den Lebensraum zu beobachten, die im April geringer ausgeprägt war als im Mai.

In beiden Monaten war die Dichte der Weibchen in pflanzenreichen Gebieten deutlich höher als in Gebieten mit spärlichem Pflanzenwuchs. Die Siedlungsdichte der Männchen war dagegen in beiden Gebieten gleich, und ihre Dichte nahm von April bis Mai ab. Konkurrenz innerhalb der Art (Männchen–Weibchen-Wechselwirkung) wurde auschließlich in dem Monat mit höherer männlicher Dichte beobachtet. In diesem Lebensraum war die Konkurrenz durch die räumliche Verteilung der Geschlechter bestimmt und weitgehend unabhängig von den strukturellen Eigenschaften der Gebiete. Ohne diese Konkurrenz war die räumliche Verteilung der Geschlechter hauptsächlich auf die Lebensraumstruktur bezogen.

Im günstigen Lebensraum begannen Weibchen und Männchen ihre sexuelle Aktivität zu Anfang der Fortpflanzungsperiode. Während beider Monate lag das Gewicht der Weibchen in den günstigen Lebensräumen höher als in den ungünstigen und zeigte darüber hinaus einen positiven Zusammenhang mit der pflanzlichen Bedeckung des Gebietes. An den Fangstellen war das durchschnittliche Gewicht der Männchen positiv mit dem der Weibchen korreliert.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNG

Foraging behavior of the Indian short-nosed fruit bat *Cynopterus sphinx*

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Receipt of Ms. 18. 06. 1998
Acceptance of Ms. 14. 12. 1998

Key words: *Cynopterus sphinx*, frugivory, foraging, telemetry

The Indian short-nosed fruit bat *Cynopterus sphinx*, one among the old world bats (Pteropodidae), inhabiting the tropics, roosts solitarily or in small groups in the foliage (Bhat and Kunz 1995). *C. sphinx* exhibits elaborate tent-roosting behaviour (Balasingh et al. 1995). The data collected to date on the foraging behaviour of *C. sphinx* are more biased to male individuals since these tent-roosting harem males exhibit several behavioural repertoires (Balasingh et al. 1993; Marimuthu et al. 1998). We carried out radio-telemetry studies on the foraging behaviour of male and female *C. sphinx* from the same habitat.

The study area, Madurai Kamaraj University campus and adjoining areas in Madurai, South India (lat 9°58′ N; long 78°10′ E) is surrounded by tall trees including *Polyalthia longifolia*, *P. pendula*, *Azadirachta indica*, *Ficus bengalensis*, *F. religiosa*, *F. benjamina*, *Bassia latifolia*, *Cocos nucifera*, *Caryota urens*, *Borassus flabellifer*, and *Mimusops elengi*. Five males and five females were radio-tagged. The foraging studies were carried out for 640 night hours (for 81 nights). Male *C. sphinx* (47 ± 3 g) chew and clip the twigs of the interior of the foliage of trees such as *P. longifolia, B. flabellifer*, and *C. nucifera* and thus make tent-roosts. Bats were captured from their tent roosts using mist nets (Avinet-Dryden, NY. 13053-1103, U.S.A.). Their body mass was recorded to the nearest 1.0 mg with a spring balance (Avinet-Dryden, NY. 13053-1103, U.S.A.) Length of forearm was measured to the nearest 0.1 mm with the help of vernier calipers. The radiotracking studies were conducted between May 1997 and March 1998. Each bat was fitted with a radiotransmitter (2.6 g) covering a range of 400–500 m, mounted over an aluminium collar covered by a light reflective tape. The transmitter along with the collar weighed only 5.5 % of the average body weight of *C. sphinx*. We used two sets of receivers and collapsible 5-element Yagi antennae (Customs Electronics, Urbana, Illinois, U.S.A.). Radiolocations were triangulated from three tracking units. Bearings were taken in as short a time interval as possible and locations with a minimum angle of interaction < 30° were discarded. The time duration between the first and last bearing used to estimate a bearing was usually < 9 min. Where ten or more locations of a bat could be triangulated, the size of the foraging area of the individual was calculated by the 'minimum range method' (Mohr 1947). Theoretical centres of activity within the foraging areas were estimated (Hayne 1949), and the distance between these centres of activity and the day roost was calculated. The study area map (Fig. 1) was divided into 20 grids of 1 km^2 area each. Horizontally it is marked 'a' to 'e' and vertically it is marked '1' to '4'. This would facilitate nam-

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Fig. 1. Typical representative triangulated foraging areas of a male, M4 (○) and a female, F1 (□) *C. sphinx*, in a grid map of the study area in Madurai, Southern India, Each grid covers 1 km^2.

Table 1. Distance between centres of foraging area and day roost for five males and five females of *C. sphinx*. FA – Foraging Area, FA1 – First foraging area, FA2 – Second foraging area, FA3 – Third foraging area.

Bat No.	Distance between the day roost to FAs (km)		
	FA1	FA2	FA3
M1.	0.12	–	–
M2.	0.10	–	–
M3.	0.09	–	–
M4.	0.20	–	–
M5.	0.10	0.50	–
F1.	2.10	0.20	0.75
F2.	1.20	0.50	0.20
F3.	1.80	0.20	0.70
F4.	2.20	0.40	–
F5.	0.20	NF	NF

ing specific foraging areas and day roost of each bat. The activity of the bats was monitored with the night vision sniperscope (Litton Precision Product, Germany, M-972) and their activity budget was calculated by monitoring the fluctuations of beep pulses from the receiver. The constant beep signals were considered as 'rest'.

All the five radio-tagged males (M1 to M5) had their respective day roost and foraging area in grid 2 b, whereas, the fifth male (M5) had an additional foraging area in 3 c (Fig. 1). Throughout our study only one male (M4) was found to have night roost fidelity and *Guetterda speciosa* was used as night roost constantly. But the other tagged bats of both sexes used more than one night roost. Each individual had used more than one tree species such as *Areca catechu, P. longifolia, A. indica, C nucifera, Achras sapota*, etc. The mean travelling distance for males was 0.22 ± 0.19 km and the mean size of the foraging area was 0.75 ± 0.27 km^2. All the females were found to be utilising more than one foraging area. Among these, one area lies far from the day roost and the other area (s) lies nearer to the day roost. For instance, F2 and F3 foraged in grids 2 b, 2 c, and 3 b; and 2 a, 2 b, and 2 c respectively, while F1 foraged in grid 2 c and two sites in 4 d. During the observation, F1, F2, and F3 regularly utilised the three different foraging areas every night. But the sequence of visits to different areas changed every night. F4 foraged only at two different foraging areas (4 b and 2 b). Interestingly, F5 roosting in grid 2 b spent < 20 % of night time (n = 68 hours observation) foraging in 2 b. The other foraging area of this bat could not be located as the foraging area was beyond 4 kms. The mean travelling distance for females was 2.1 ± 1.0 km and the mean size of the foraging area was 0.83 ± 0.12 km^2. The males and females exhibit a high level of activity during the early hours of night soon after emergence and another activity peak during pre-dawn hours (Fig. 2).

Our study shows that the foraging pattern of *C. sphinx* is similar to that of *Artibeus jamaicensis, Phyllostomus hastatus*, and *Carollia perspicillata* (August 1981; Fleming 1988; McCracken and Bradbury 1981; Morrison 1978). Bats leave the day roost shortly after sunset and fly to foraging areas while they begin to search for ripe fruits. The harvested fruits were transported to the "night roosts" for consumption. These "night roosts" might promote digestion and energy conservation, offer retreat from predators, serve as centres for information transfer about the location of fruit patches and facilitate social interaction (Kunz 1982). A regular travel path exhibited by M 4 between day roost and foraging area may be attributed to the constancy of resource availability. Such a "trap-lining" behaviour minimizes search distances and energy cost (Kunz 1982).

It seems clear that the male *C. sphinx* restricts its foraging areas closer to the day roost. Since the males involve in tent construction, harem formation and defence, a short distance foraging area would promote harem defence near the day roost (Fleming 1988; Marimuthu et. al., 1998). This observation of short distance foraging flights of males is consistent with observations of the harem males of *A. jamaicensis, P. hastatus* and *C. perspicillata* where feeding predominantly occurs in the vicinity of their day roost (Fleming 1988; Hardley and Morrison 1991; McCracken and Bradbury 1981; Morrison 1979; Morrison and Morrison 1981). The foraging areas of males are overlaping because the day roost of most of the males lies within a rich food patch. The reasons for the commutation to longer distances, spending more time and utilization of several foraging areas of female bats are not clearly known. One of the reasons for long distance commutation by females might be search for potential male tent roost and to assess the harem male's parental ability. Furthermore, they change their primary foraging area in an unpredictable fashion as observed in *C. perspicillata* (Kunz 1982). Since not every foraging area contains the same potential food source, one reason for such unpredictable "visits" might be to increase dietary diversity. In the usual bimodal pattern of activity, maximum foraging bouts occurred in the early hours of the night and lesser activity during the pre-dawn hours (Fleming 1982). *C. sphinx* also shows a similar pattern of activity.

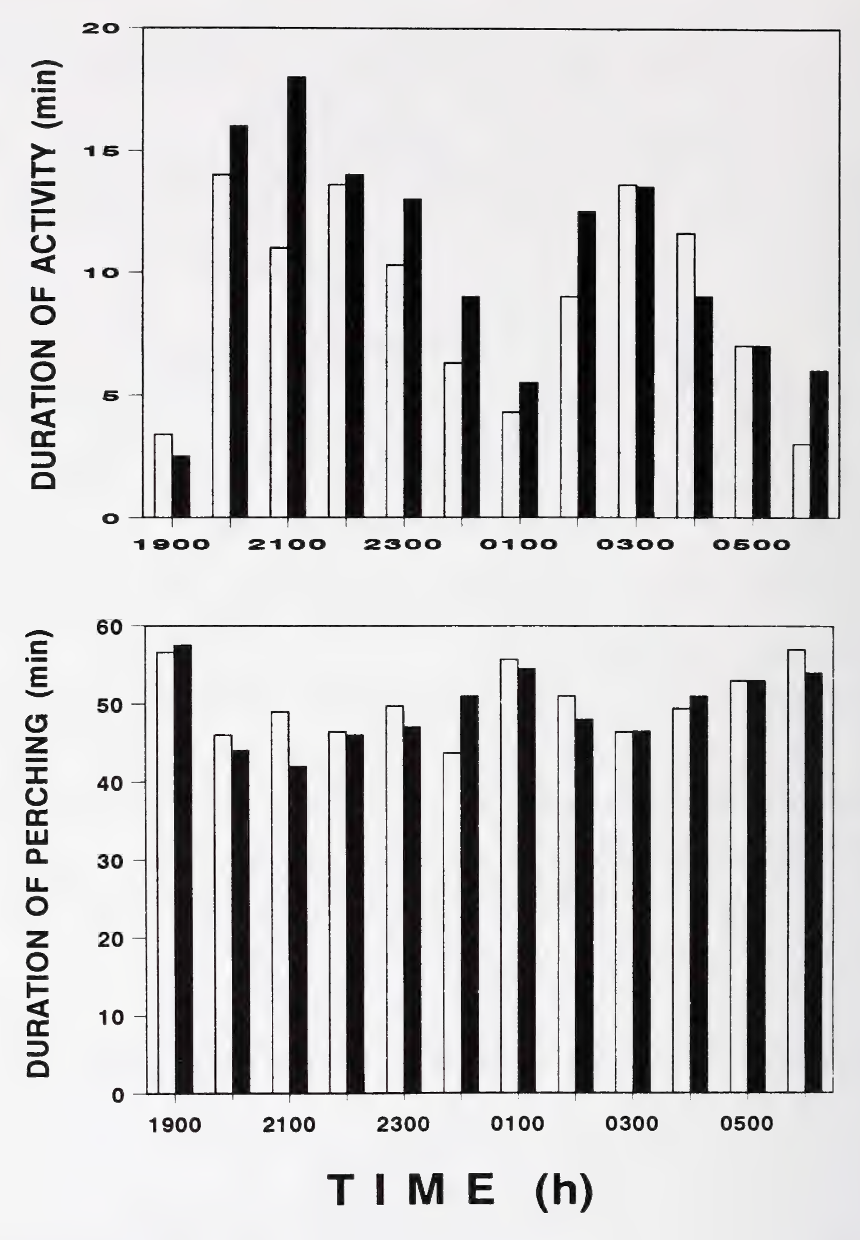


Fig. 2. *a)* Duration of activity and *b)* duration of perching for radio-tagged *C. sphinx* (□ – Male and ■ – Female)

Acknowledgements

We are grateful for the financial assistance from DOEn to RS (14/11/94-MAB/RE), CSIR to GM (37(861)/94/EMR-II) and SRF (CSIR) to VE.

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Buchbesprechung

ANONYMUS: **Die Nashörner. Begegnung mit urzeitlichen Kolossen.** Fürth: Filander Verlag 1997. Zahlreiche Abb. und Farbtafeln, geheftet, 258 pp. DM 68,–. ISBN 3-930831-06-6.

Schon auf der Titelseite gerät der Leser in Verwunderung: Ein Herausgeber für diesen Band wird nicht genannt! Ferner werden die Nashörner im Buchtitel als „urzeitliche Kolosse“ bezeichnet, obwohl in dem vorliegenden Werk nur in einem Beitrag von C. P. GROOVES fossile Rhinocerotoidea behandelt werden; alle anderen Kapitel beschäftigen sich mit rezenten Arten.

Der Band enthält 20 Kapitel, welche von verschiedenen Autoren verfaßt wurden. In den vier einleitenden Abschnitten werden die Beziehungen zwischen Mensch und Nashörnern dargestellt, dann folgt der schon erwähnte Abschnitt über die Stammesgeschichte und Verwandtschaft und jeweils einer über die Körperbeschaffenheit, sowie über das Verhalten der Arten.

Zehn Kapitel bilden den Hauptteil des Bandes: Angaben zum Erscheinungsbild der Arten, durch Farbabbildungen illustriert, sowie Bemerkungen zur Biologie, zum Verhalten und zur Verbreitung (durch Karten gut illustriert) werden geboten. Der Leser findet in diesen Kapiteln gute Darstellungen der fünf rezenten Arten der Familie Rhinocerotidae. Die drei asiatischen Arten werden in jeweils eigenen Kapiteln behandelt: Das Sumatra-Nashorn (*Dicerorhinus sumatrensis*) wird vorgestellt, das Java-Nashorn (*Rhinoceros sondaicus*) beschrieben, und ein Artikel über das Indische Panzernashorn (*Rhinoceros unicornis*) folgt. Den beiden afrikanischen Nashornarten sind jeweils mehrere Kapitel gewidmet. In drei Darstellungen wird ein umfassendes Bild des Spitzmaul-Nashorns (*Diceros bicornis*) geboten, wobei nicht nur die Biologie der Art, sondern auch der Gesamtbestand und sein Schutz behandelt werden. Dem Breitmaul-Nashorn (*Ceratotherium simum*) sind vier Kapitel verschiedener Autoren gewidmet.

Den letzten Teil des Buches füllen Darstellung des Handels mit Nashornprodukten, sowie Übersichtsdarstellungen des Nashorn-Schutzes und der Erhaltungsmaßnahmen, ferner werden Bemerkungen zu „Nashörnern im Zoo heute“ gemacht. Ein entbehrliches Kapitel schildert die Tätigkeit eines kenyanischen Aktivisten, der sich dem Schutz von Nashörnern verschrieben hat. Eine kurze tabellarische Zusammenstellung von vergleichenden Daten zu allen fünf Arten, sowie eine unnötig langatmige Vorstellung der am vorliegenden Band beteiligten Autoren und ein nützlicher vierseitiger Index schließen den Band ab.

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Subscription rate (1999): Price per volume: DM 478.00*; UK Sterling 192.00
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Printed in Germany

Printed on acid-free paper effective with vol. 61, no. 1, 1996.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



ISSN 0044-3468 · Z. Säugetierkunde · 64(1999)4 · S. 193-256 · August 1999

URBAN & FISCHER

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1999

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Z. Säugetierkunde **64** (1999) 193–200

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

On the reproduction biology of otters (*Lutra lutra*) from Denmark

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Receipt of Ms. 20. 07. 1998
Acceptance of Ms. 29. 03. 1999

Abstract

The reproduction in Danish otters was inferred from examination of reproductive organs from 242 carcasses collected between 1982 and 1996. Estimated months of birth of collected cubs and evidence of breeding, determined in female reproductive organs, showed distinct seasonal patterns. 82 % of the cubs were born during summer and autumn months from June to November, although litters were born throughout the year. Mean litter size at birth was 1.7 ± 0.9 cubs per litter. Adult male otters showed continuous mating preparedness. No seasonal variation in paired testes weight for adult males was determined and males with high density of spermatozoa in testes smears occurred throughout the year. Adult males with spermatozoa present had a significantly higher body condition index compared to males without spermatozoa. As the imminent factor determining the breeding chronology, fish densities peaked in autumn, coinciding with maximum energetic demands on reproductive active females during the lactation period.

Key words: *Lutra lutra*, breeding pattern, reproduction, Denmark

Introduction

Otters (*Lutra lutra*) living in different areas and habitats show large variation in the breeding pattern varying from an even distribution of births throughout the year (Stephens 1957; Sidorovich and Tumanov 1994) to a strictly seasonal occurrence (Erlinge 1967; Kruuk et al. 1987). In several populations, births have been reported throughout the year with a seasonal peak (Stubbe 1969; Wijngaarden and Peppel 1970). Temporal and spatial fluctuations in the availability of food resources determine birth patterns, timing the period of highest energetic requirements of reproductive females at peak lactation with maximum fish densities (Kruuk et al. 1987; Oftedal and Gittleman 1989; Heggberget and Christensen 1994).

Most studies focus on reproductive activities and status of females and cub recruitment (e. g. Sidorovich 1991; Beja 1996; Ansorge et al. 1997). Only short notes on male mating preparedness have been published (Heggeberget and Christensen 1994; Sidorovich and Tumanov 1994). Further knowledge, on male reproductive capacity and mating preparedness in seasonally and non-seasonally breeding populations, is important for conservation and management of otters.

In Denmark, otters are known to breed throughout the year (Jensen 1964), however, no detailed information on seasonal distribution of births and reproductive phases has been presented. The aim of this study is to investigate the breeding pattern in Danish otters.

0044-3468/99/64/04-193 $ 12.00/0

Material and methods

Otter carcasses were collected between 1982 and 1996 in northern Jutland representing the main distribution area of the Danish otter population. Specimens originated from inland freshwater habitats and marine habitats with brackish waters. The majority of otters were killed in traffic. Mortality rates and the probability of finding otter carcasses were assumed to be the same throughout the year. Collection of adult otters was randomly distributed through seasons (n = 113, $\chi^2 = 5.7$, n.s.). Juveniles and subadults were collected primarily during autumn (n = 129, $\chi^2 = 44.3$, $P < 0.01$). Carcasses were subjected to a detailed necropsy and examination of health condition (Madsen 1996). Specimens were aged as juveniles (younger than 5 months), subadults and adults (older than 18 months) on skeletal criteria (Mason and Madsen 1993). Body condition index (CI) for the otters was calculated as the relation between body weight and total length according to Kruuk et al. (1987).

Age of juveniles was assessed from body weight (Stephens 1957), after calculating body weight from total length at normal body condition index (Kruuk et al. 1987). To establish female reproductive status length and diameter of uteri were measured and ovaries and uteri examined macroscopically of presence of corpora lutea, embryos, and placental scars (Heggberget 1988). Uterus horns were flushed with 2 ml water to collect blastocysts. The birth time of litter born by females was assessed from the colour of placental scars and appearance of the uterine tissue. Initially after birth implantation sites have dark pigmentation, while in the final stages implantation sites gradually become orange and white (Heggberget and Christensen 1994). Based on examination of a female killed with a cub at about 3 months of age, dark placental scars are estimated to persist for at least 3 months. Male reproductive capacity was assessed by paired testes weight including epididymes, and microscopic examination for presence of spermatozoa in testes smear (Madsen and Rasmussen 1985). Relative occurrence of spermatozoa in smear was valued as: none, low or high density. Determination of all parameters in all specimens was not possible.

Seasonal densities of fish were determined by electrofishing at 5 freshwater localities (Taastrøm and Jacobsen 1999).

Results

Juveniles

Seasonal distribution of estimated time of birth for the collected cubs is shown in figure 1. The seasonal distribution of births was significantly different from an even distribution (n = 22, $\chi^2 = 48.8$, $P < 0.001$); 82 % of the cubs were born in summer and autumn

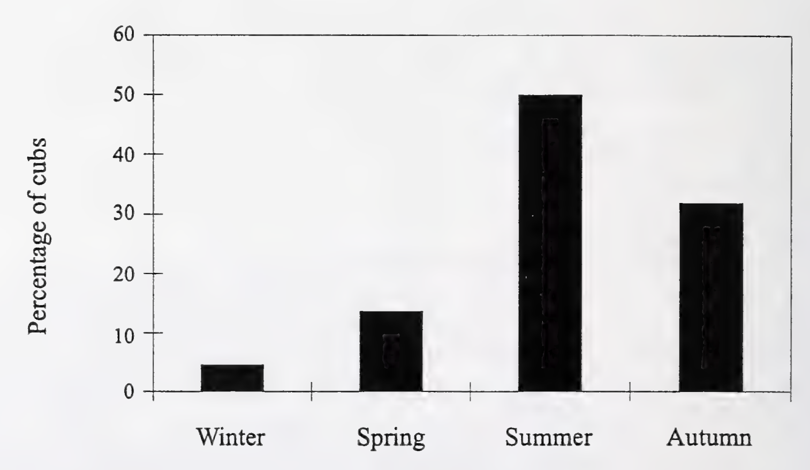


Fig. 1. Seasonal distribution of births for received Danish otter cubs (n = 22). Ages were assessed from body weight (Stephens 1957; Kruuk et al. 1987). Winter: December–February; Spring: March–May; Summer: June–August; Autumn: September–November.

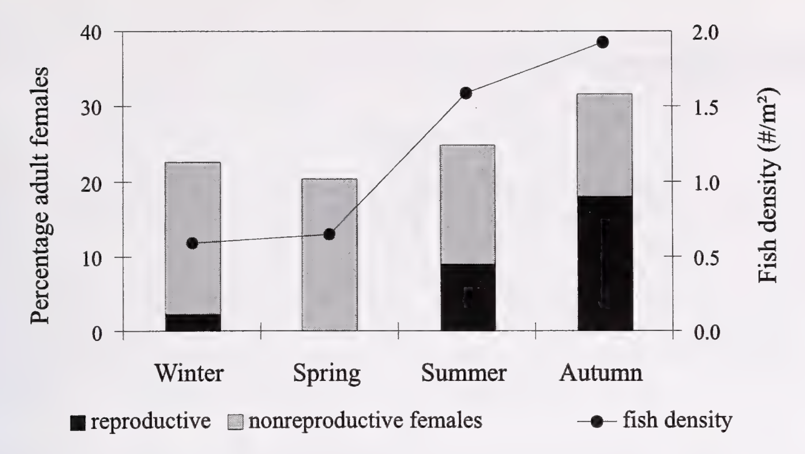


Fig. 2. Seasonal percentage of adult females with dark placental scars and fish densities in Danish freshwater habitats (TAASTRØM and JACOBSEN 1999). Percentages of reproductive females were calculated from numbers of all adult females collected each season (Winter, n = 10; Spring, n = 9; Summer, n = 11; Autumn, n = 14).

months from June to November. Highest frequency of births was seen in the three-month period of July, August, and September: 59 % in total. Siblings were counted as one.

Females

Distribution of reproductive females with dark placental scars varied seasonally (n = 13, $\chi^2 = 73.3$, $P < 0.001$) peaking in autumn and winter (Fig. 2). In all females with placental scars, uterus had regressed to normal size (HEGGBERGET 1988). Assuming parturition some two months earlier, these litters were born during the summer and autumn months corresponding with the main birth months of the cubs. Seasonal occurrence of reproductive females exhibited a good correlation with seasonal fish densities in different freshwater habitats in Denmark (Fig. 2) (TAASTRØM and JACOBSEN 1999).

Additional indications of reproductive activities determined from adult females correspond with estimated births in summer and autumn; a female killed in March had neck wounds and spermatozoa in her reproductive tract, and one pregnant female with small embryos was collected in April, and a female killed in January had old faded placental scars.

Three females had placental scars of different colours possibly indicating abortion or resorption of embryos. Overall, indications of breeding were found in 34 % of all adults. Based on numbers of embryos and newest placental scars, the average litter size was 1.7 ± 0.9, range 1 – 4 (n = 15). Including all placental scars the estimated litter size was 2.2 ± 1.2, range 1–4 (n = 15). Counts of corpora lutea resulted in litter sizes of 2.7 ± 1.7, range 1–5 (n = 7). No blastocysts were recovered. Seasonal variation of the body condition index of all adult females was not significant (n = 45, F = 1.01, P = 0.40) and no differences in body condition indices between reproductively active and nonreproductive females were established (n = 45, t = 0.405, P = 0.69).

All females classified as adults had mature reproductive organs. Alterations of reproductive organs were observed in four adult females. One female had severely convoluted uterine horns. One female had fibrous but normal sized uterus with two cysts on the uterus and an occlusion in the uterine body. Two females had small uterine cysts. No placcutal scars, embryos or corpora lutea were recorded in these four females. Immature females had thin and translucent uterine tissue. Some females aged as subadults showed

maturing uteri and had large follicles in ovaries. They were collected at all seasons, but most frequently in spring (n = 16, $\chi^2 = 41.4$, $P < 0.01$).

Males

Paired testes weights of adult, subadult, and juvenile males differed significantly (Tab. 1). Within age classes specimens with different densities of spermatozoa showed different paired testes weights.

Adult males with spermatozoa in low and high densities were found throughout the year. Seasonal variation in paired testes weight for all adults was not found (n = 56, F = 0.31, P = 0.81) (Fig. 3), nor was any trend apparent for males with spermatozoa present (n = 48, F = 0.09, P = 0.97). No seasonal variation in body condition index occurred (n = 55, F = 0.51, P = 0.68). Paired testes weight and body condition index of adult males

Table 1. Paired testes weights for different age classes of male otters ($^{a}P < 0.001$). Paired testes weights for testes with different densities of spermatozoa within an age class($^{b}P < 0.001$ and $^{c}P < 0.01$).

Age class	n	Mean ± SD (g)	Range (g)
Adults	59	10.8 ± 3.4^{a}	3.8 – 17.4
high	31	12.7 ± 2.8^{b}	6.4 – 17.4
low	15	9.3 ± 2.2^{b}	4.8 – 13.0
non	8	7.1 ± 2.9^{b}	3.8 – 12.2
Subadults	47	5.5 ± 3.2^{a}	0.9 – 12.4
high	8	9.8 ± 1.2^{b}	8.1 – 12.4
low	17	$6.1 \pm 2.6^{b,c}$	2.0 – 11.2
non	22	3.7 ± 2.5^{c}	0.9 – 9.8
Juveniles	10	0.9 ± 0.5^{a}	0.1 – 1.6

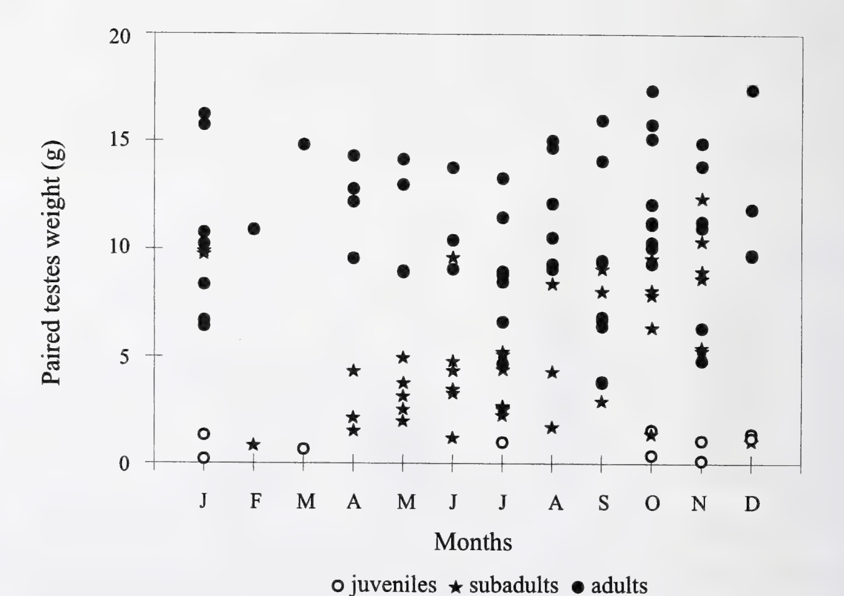


Fig. 3. Monthly variations of paired testes weights among Danish male otters (n = 115).

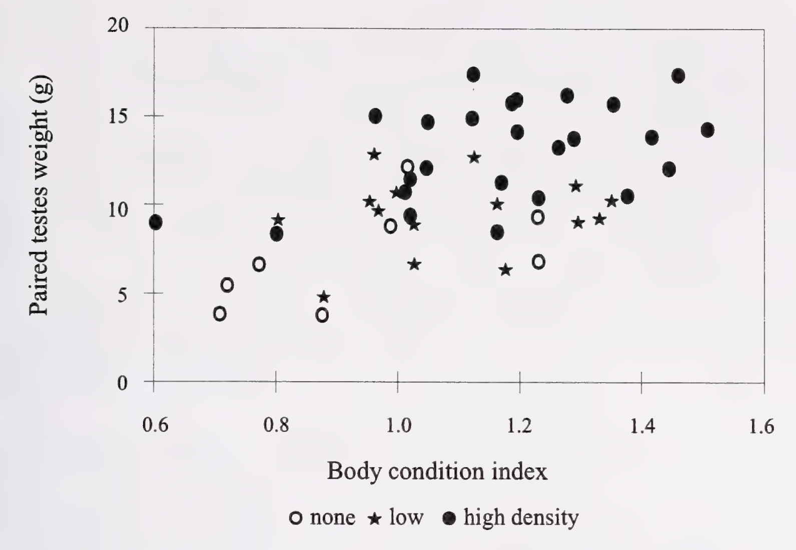


Fig. 4. Paired testes weight and body condition indices for adult Danish male otters (n = 48). Densities of spermatozoa are indicated as none, low, and high. Body condition index is in accordance with KRUUK et al. (1987)

were significantly correlated (n = 48, t = 3.38, P < 0.001) (Fig. 4). Adult males with spermatozoa present showed higher body condition indices than males without spermatozoa (n = 48, F = 18.8, P < 0.001).

For subadults with immature testes and no spermatozoa present, no differences between seasonal testes weights were established (n = 22, F = 0.22, P = 0.88). Paired testes weight for subadults with spermatozoa present varied throughout the seasons, peaking during winter (n = 23, F = 5.68, P < 0.01). Subadult males with high density of spermatozoa in the testes (n = 8) were found only among specimens collected in autumn and winter. The findings of subadults with high densities of spermatozoa indicate that maturation may occur at an age of 18 months.

No seasonal variation in body condition index (n = 53, F = 0.77, P = 0.68) was established among subadults. Despite different stages of sexual maturity in this age group, paired testes weight and body condition were significantly correlated (n = 42, t = 2.84, P < 0.01) and subadults with spermatozoa present had significantly higher body condition indices (n = 42, F = 7.24, P < 0.05).

Discussion

Reproductive phases of females and cub recruitment have been examined in other populations. Litter sizes in Germany based on counts of corpora lutea reached 2.8. Based on embryos and placental scars they were 2.7 and 2.1 based on observed cubs per litter (ANSORGE et al. 1997). In a Belarussian population, litter size was 2.7 at corpora lutea phase, 2.6 cubs less than one month of age and 2.4 cubs following females (SIDOROVICH 1991). Similar numbers of corpora lutea were counted in Danish otters, but the implantation frequency was lower and loss of embryos during gestation higher (20 %). An equivalent frequency of resorption or abortion of implanted embryos has been reported in Norwegian otters (HEGGBERGET and CHRISTENSEN 1994). Litter sizes estimated from numbers of embryos and placental scars in females represent maximum litter size at birth (STRAND et al.

1995). Postnatal mortality rates between 12 % and 24 % further reduces litter sizes (Sidorovich 1991; Heggberget and Christensen 1994; Ansorge et al. 1997). Danish otters produce smaller litters compared to litter size estimated from observations of family groups in marine habitats (Kruuk et al. 1987; Heggberget and Christensen 1994; Beja 1996), and noticeable smaller litters than generally reported from freshwater habitats (Wijngaarden and Peppel 1970; Mason and Macdonald 1986; Beja 1996; Ansorge et al. 1997). Relatively low recruitment due to small litters in the Danish otter population is compensated by a higher proportion of reproductive active females (34 %), compared to 23 % of adult females in the stable high density freshwater population in the eastern part of Germany (Ansorge et al. 1997).

Otters living in adjacent freshwater and marine habitats may have different breeding chronology and litter sizes (Beja 1996). Within an individual otter's home range, however, utilisation of freshwater and marine centres vary depending on food availability (Sjöåsen 1997), and a separation of Danish populations in strictly marine or freshwater living otters would be questionable.

The continuous mating preparedness in adult males is consistent with unseasonal oestrus and ovulation bouts in females (Heggberget and Christensen 1994). Adult males with poor body condition indices and low paired testes weights all suffered from various infectious diseases (Madsen 1996) or were collected during a severe winter. The latter had probably lost conditions rapidly and still had spermatozoa present in testes.

As in this study, a considerable range in paired testes weights with spermatozoa was found in a small number of adult males from Russia and Belarus (Sidorovich and Tumanov 1994). Maturation at 18 months in Danish otters was equivalent to age of maturation observed in Germany (Stubbe 1969). In Russia and Belarus Sidorovich and Tumanov (1994) found immature testes in all 1–2 year old males, and in Norway females matured between 2 and 3 years of age (Heggberget 1988).

Paired testes weight appears to be a sufficient measurement of testicular activities for large samples, but with apparent differences in testes weights between populations and a wide weight range within populations, conclusions on mating preparedness in male otters from testes weights data alone must be interpreted cautiously.

Continuous oestrus cycle and non-seasonal breeding potential in otters may have evolved as a reproductive risk-reducing adaptation to an unpredictable, although seasonally changing environment (Heggberget and Christensen 1994). Additional adaptation to annual fluctuations of the environment include flexible population dynamics with social regulation of recruitment and population density-dependent fecundity of females (Kruuk et al. 1991; Sidorovich 1991). Seasonal variation in body condition of females correlated with food availability and breeding success on the Norwegian coast (Heggberget and Christensen 1994).

Assessed by the invariability of body condition index for Danish otters, food resources appear relatively stable. However, a seasonal birth peak has evolved correlating maximum energetic strain on reproductive females with peaking fish densities in Danish freshwaters.

Acknowledgements

We gratefully acknowledge H. H. Dietz at the Danish Veterinary Laboratory and the taxidermists at the Natural History Museum, Århus and the Zoological Museum, Copenhagen, for assistance with the autopsy and preservation of specimens. We also acknowledge B. Gaardmand and M. Hammershøj for technical assistance and K. Zaluski for linguistic help. H. Weber wrote the German summary. T. M. Heggberget and the anonymous reviewers are acknowledged for valuable comments on the manuscript.

Zusammenfassung

Über die Fortpflanzungsbiologie von Fischottern (Lutra lutra) in Dänemark

Die Geschlechtsorgane von 242 Totfunden dänischer Otter aus den Jahren 1982 bis 1996 wurden im Hinblick auf den Reproduktionszustand des jeweiligen Einzeltieres untersucht. Diese Ergebnisse ließen Rückschlüsse auf die Fortpflanzungsbiologie der dänischen Otterpopulation im Vergleich zu den aus der Literatur bekannten Mustern von Otterpopulationen anderer Länder zu.

Der Nachweis erfolgter Geburten anhand von makroskopischen Untersuchungen weiblicher Geschlechtsorgane wies deutlich saisonale Unterschiede auf. Schätzungen des Geburtsmonats tot aufgefundener Jungtiere konnten diese Saisonalität noch untermauern: 82 % der Jungtiere wurden in den Sommer- und Herbstmonaten zwischen Juni und November geboren, wobei grundsätzlich Geburten zu allen Jahreszeiten nachgewiesen werden konnten. Die durchschnittliche Jungtieranzahl betrug 1,7 ± 0,9 zum Zeitpunkt der Geburt.

Adulte männliche Otter scheinen im Allgemeinen das ganze Jahr über paarungsbereit zu sein. Zwar wurden Schwankungen der Spermiendichte im Hodensekret adulter Männchen festgestellt, diese konnten jedoch ebensowenig wie die ermittelten Hodengewichte saisonalen Mustern zugeordnet werden. Dagegen bestand eine signifikante Korrelation zwischen dem Hodengewicht und dem Konditionsindex, wobei adulte Männchen mit im Hodensekret enthaltenen Spermien höhere Konditionsindizes aufwiesen. Saisonale Variationen der Konditionsindizes aller Otter für verschiedene Altersgruppen, Männchen oder Weibchen, konnten nicht beobachtet werden.

Beziehungen zwischen der Hauptphase der Jungtieraufzucht und der Fischdichte der dänischen Gewässer waren auffällig. Letztere erreicht ihren Höhepunkt im Herbst, die Zeit des maximalen energetischen Bedarfs laktierender Otterweibchen. Somit ist anzunehmen, daß die Fischdichte einen bedeutenden Faktor für die Saisonalität der Reproduktion dänischer Otter darstellt.

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Otter *Lutra lutra* predation in cyprinid-dominated habitats

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Receipt of Ms. 18. 08. 1998
Acceptance of Ms. 10. 03. 1999

Abstract

Diet composition of otter *Lutra lutra* was quantified by analysis of 2 048 spraints collected at half-month intervals concurrently with a one year culture cycle of carp *Cyprinus carpio* in a fish pond area (S.E. Poland) and compared with data on farm stocks. Presence of cultured fish affected the diet composition, carp being the single most important food. The estimated biomass proportion of carp in spraints varied monthly between 15.7 % in June and 78.0 % in March. Carp abundance changes could not explain the seasonal variation in predation pressure. The factors responsible for the seasonal shifts in the use of resources are discussed.

Key-words: *Lutra lutra*, predation, cyprinids, thiaminase, fish-ponds

Introduction

Freshwater populations of the Eurasian otter *Lutra lutra* (Línne, 1758) have suffered a substantial decline in many European countries, this being related to some aspects of human management of aquatic ecosystems (Mason 1989). Although most of the man-made changes are regarded as detrimental to otters, some developments in freshwater habitats dominated by culture-based fisheries may contribute to an increase of food resources. Local strongholds for otter populations have been reported in association with aquaculture sites in central Europe (Macdonald 1995), but the scientific data on the interactions between these populations and farm stocks are lacking. There is a clear need for research on dietary patterns of otters in such man-modified habitats (Mason 1989), even more so because it is suggested that otter numbers are limited by fish populations (Kruuk et al. 1993). In central and eastern Europe aquaculture is dominated by cyprinids, stocked in large earthen ponds, which are very difficult to protect against predators. In Poland only the common carp *Cyprinus carpio* contributes to more than 95 % of the overall aquaculture production and there is growing concern over possible depredation of farm stocks by otters (Dobrowolski et al. 1995).

Cyprinid aquaculture sites create a specific habitat dominated by one prey category for otters. Abundance of food supply is governed by fish culture regime. Moreover, cyprinids exhibit high thiaminase activity, an enzyme that catalyzes the cleavage of thiamine – vitamin B_1 (Harris 1951). The aim of this study was to quantify seasonal variation in otter diet composition at cyprinid fisheries and to gather information on factors influencing the exploitation of farm stocks. The research was conducted in a carp-pond area in southeast Poland.

0044-3468/99/64/04–201 $ 12.00/0

Material and methods

Study area

The study areas were the Tyśmienica and Prokop (hereafter Tyśmienica) fish-ponds and adjoining bodies of water situated in the upper and middle regions of the Tyśmienica River 22°50′–52′E, 51°32′–33′N, Lublin Province, S.E. Poland, an area of about 2 400 ha. Tyśmienica valley is covered by grasslands and bounded from the east by coniferous woodlands. Its climate is influenced by continental factors with marked seasonal temperature and percipitation changes.

Semi-intensively cultivated ponds, up to 1 km wide along the Tyśmienica, are managed by two fish-farms, but spatially they constitute one complex. Farming comprised 19 ponds (1 to 18 ha area, 1.0–1.5 m deep) with a total water surface of 127.5 ha, seven of them stocked with 1+ (fish in their second year of life) carp and the others with 0+ (fry) carp. The associated waterflows are up to 5 m wide and up to 1.5 m deep. Because of high bacteriological and organic contamination of the Tyśmienica River the number of fish species has decreased dramatically during the last twenty years (Radwan and Girsztowtt 1994).

Despite the obvious degradation of the Tyśmienica valley, otters are widely reported by local fishermen to have occurred there for many years. During the present research no otter deterrence was undertaken by the fish-farms. American mink *Mustela vison* have not been recorded in the study area.

Farm stocks

As a warm-water species, carp plays a role in the riverine habitats of S.E. Poland only in artificially stocked sites. As otters normally spraint close to their feeding sites (Kruuk 1995), it is most likely that spraints collected in the study area represented prey items consumed at Tyśmienica ponds. However, their ranges may have incorporated other carp farms located up to a few tens of km along the waterways away from Tyśmienica.

Research on otter predation covers a one-year seasonal cycle of carp (0+ and 1+) culture between April 1994 and March 1995, therefore data are presented in this order. The local fisheries' managers provided information on fish supply for each pond. Assessment of carp abundance was based on the data from stocking and restocking operations, and routine net sampling twice a month between June and October. No fishing was undertaken between November and February as the ponds were temporarily frozen. The missing figures were estimated with the help of the fish-farm ichthyologists, assuming a constant mortality rate and weight decrease of young carp during winter.

The term 'farm fish' refers only to carp. The 'unplanned breeding' and the accompanying species in some of the fry ponds: wels *Silurus glanis* and pike *Esox lucius* fry (together 0.7 % of the total fish biomass at harvesting) were not taken into account in the statistical analysis.

Access to ponds was assessed by measuring the ice cover and relating it to the whole pond water surface twice a month between November 1994 and March 1995.

Spraint sampling and analysis

Otter diet was assessed by spraint analysis. Spraints were collected at ponds and along water courses adjoining the ponds. Standard collection routes, totaling about 14 km, were visited twice each month between April 1994 and March 1995. Faecal material was wrapped in individual bags, dried, and washed through a 0.5 mm sieve. Prey remains were identified using a reference collection and existing keys. 'Key bones', the species-specific hard parts that occurred with the greatest frequency in spraints, were used to assess the size of prey items represented in the spraints. They were measured to the nearest 0.5 mm using an ocular micrometer. Key bones comprised pharyngeal teeth structures, maxillae, and dentaries (cyprinids, cobitids); preoperculae, operculae, and jaws (percids); operculae, premaxillae, and dentaries (gasterosteids) and dentaries, articularies, and operculae (other taxa). Measurements from individuals collected in the study area were regressed against original total fish lengths and these against fish fresh masses to produce conversion equations for carp (separately for both age classes) and species dominating in the otter diet. The relationships for less common fishes were taken from the literature, mainly Libois et al. (1987).

Amphibian key bones were ilea, frontoparietale, and jaws while body masses were estimated from

a reference collection by adopting three weight classes for each species. Body lengths of crayfish *Astacus astacus* individuals were estimated from chela widths and lengths of the anterior part of cephalothorax with the regressions of Podsiadło and Olech (1994) and length-weight relationship with equations from Stypińska (1978). Since it was often impossible to assess crayfish body length from broken pieces retrieved from spraints, data based on remains of predated crayfishes found on river banks were extrapolated to the entire half-month sample. Bird and mammal remains were assigned to the family level by examining hair and feather characteristics (Day 1966; Brom 1986). Mean weights of the most common species of these families observed at Tyśmienica ponds, taken from Cramp and Simmons (1977) and Myrcha (1969) were applied.

Prey proportions estimation

Prey proportions in the diet were assessed by the method of relative weight percentages with total weight of individuals of a prey category, expressed as a percentage of the total weight of all prey individuals (Bekker and Nolet 1990). The number of individuals of a species represented in a spraint was scored as the highest total of any of the key bones present. Crayfish and bird numbers were defined as the highest totals of any of the identifiable parts present in the whole half-month sample. Insects smaller than 1 cm were considered an effect of secondary ingestion and omitted. Carp fraction in samples was also expressed in terms of frequency of occurrence – the percentage of spraints where a prey category occurred (Bekker and Nolet 1990).

Monthly changes in calorific values of 'averaged' otter food per weight unit were estimated. Relative calorific values of prey categories (Tab. 1) were used combined with data on digestibility (as the percentage of the total ingested food available to the predator as energy). Data on digestive efficiency (50 % for invertebrates, 70 % for fish and 80 % for other vertebrates) were assumed following Beja (1996). Furthermore, prey species were divided into thiaminase-free and thiaminase-active. Data on thiaminase presence were obtained from published reviews (Tab. 1).

Non-parametric tests were used throughout as most of the analyzed variables did not meet the assumptions of normality or homogeneity of variances. The trophic niche breadth was estimated using Levins' measure $B = 1/\Sigma p_i$, where p_i is the percent occurrence of a general prey taxa (Levins 1968).

Table 1. Main food categories for otters in the Tyśmienica valley: energy content and thiaminase presence. Mean energy content of crayfish and fish prey after Scherz and Senser (1989), except cobitids (Klejmenov 1962), ictalurids (Feunteun and Marion 1994) and gasterosteids (Massias and Becker 1990); values of other non-fish prey from Griffiths (1977), except mammals (Myrcha 1969). Some data have been recalculated to kJg^{-1} wet weight from the original sources. Data on thiaminase activity after Harris (1951), Tatarskaya et al. (1954) and Ender (1966). If no relevant data for a given species were available from the literature, they were taken from the closest related taxa.

Food items	Energy content (kJg^{-1} wet weight)	Antithiamine activity
Insects	4.53	–
Crayfish	2.95	–
Pike	3.73	+
Carp	5.22	+
Other cyprinids	4.67	+
Cobitids	4.55	+
Ictalurids	4.20	+
Gasterosteids	3.32	+
Percids	3.71	+
Amphibians	4.18	–
Waterbirds	4.43	–
Mammals (soricids)	4.24	–

Results

8437 prey individuals were represented in 2048 spraints. Otters fed primarily on fish, composing more than 90 % of food in all months except in June–September (44.3 %–73.6 %) and January (82.6 %). On an annual basis carp formed 40.8 % of the estimated consumed biomass being the major component in the otter diet during all months (Fig. 1) except June. However, its contribution to otter diet varied from the relatively lowest values in summer (15.7 % by weight and 18.0 % by frequency in June) and in the coldest months, December–January (21.1 %–23.4 % by weight and 17.2 %–19.7 % by frequency) to a peak in March when carp made up 78.0 % of the estimated consumed biomass and was found in 68.6 % of spraints. Monthly estimates of carp use in terms of biomass and frequency of occurrence were similar ($r = 0.92$, $n = 12$, $p < 0.001$).

Percids (ruffe *Gymnocephalus cernua* and perch *Perca fluviatilis*), making up an annual mean of 13.7 % of biomass and cyprinds (mainly gudgeon *Gobio gobio*) with 12.3 % formed the largest proportion of wild fish recorded in the otter diet. Estimates of wild fish proportion ranged from 19.6 % in March to 72.3 %–59.2 % in December–January. Wild fish species represented in spraints were smaller than carp throughout the year. Even in June, when the difference was the smallest, carp was significantly larger (Mann-Whitney U-test; $u = 323.0$, $p < 0.001$). The estimated mean length of wild fish prey was 7.2 ± 2.5 (SD) cm with the median length of 7.0 cm ($n = 5545$). The mean length of carp was 11.4 ± 2.6 cm with the median of 10.9 cm ($n = 1249$).

In summer, crayfish and waterbirds (Podicipedidae, Rallidae) constituted a substantial part of otter food. In June, crayfish was the principal prey species with 22.3 %. Amphibians (frogs *Rana 'esculenta'*, *R. temporaria*, *R. arvalis*) were taken by otters during all seasons, but made a significant contribution only in January reaching 16.5 %. Mammals and insects were of negligible importance (0.01 % on an annual basis).

Carp abundance in terms of biomass varied up to 6.6-fold in the course of the year but these changes were not significantly correlated with estimates of the contribution to the diet of otters in terms of either weight ($r = 0.24$, $n = 12$, $p = 0.44$) or occurrence ($r = 0.16$, $n = 12$, $p > 0.71$; Fig. 2). There was an inverse correlation between proportion of carp in spraints and the extent of ice cover at ponds ($r = -0.79$, $n = 7$, $p < 0.05$ for both biomass and occurrence; Fig. 3), while positive and non-significant relationships were

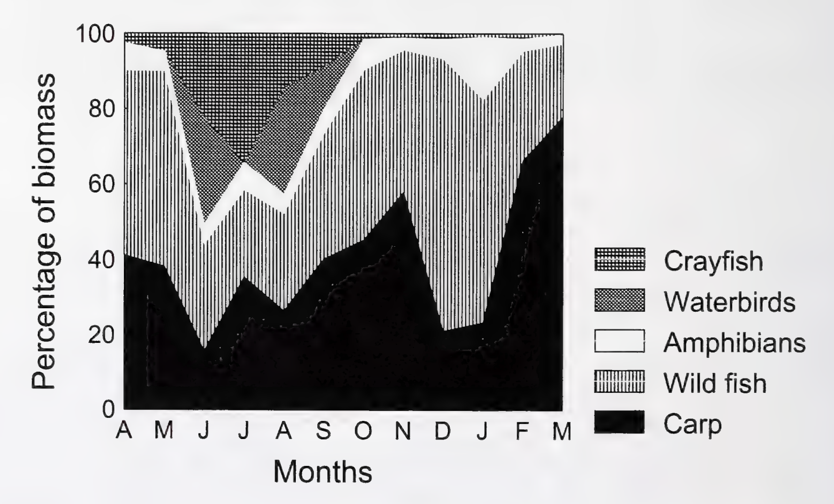


Fig. 1. Monthly variation in the estimated proportion of major prey categories in otter diet in Tyśmienica ponds area, April 1994–March 1995, quantified in terms of weight.

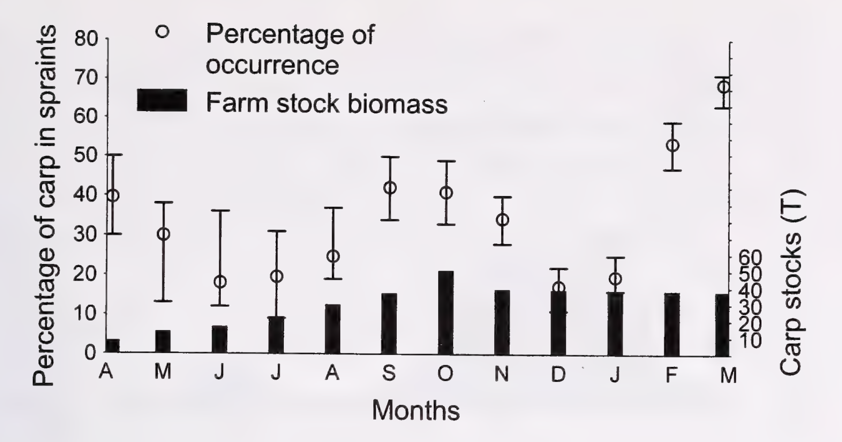


Fig. 2. Frequency of occurrence (with 95 % confidence intervals) of carp in otter spraints and changes in the total abundance of farm stocks in the Tyśmienica fish-ponds, April 1994–March 1995.

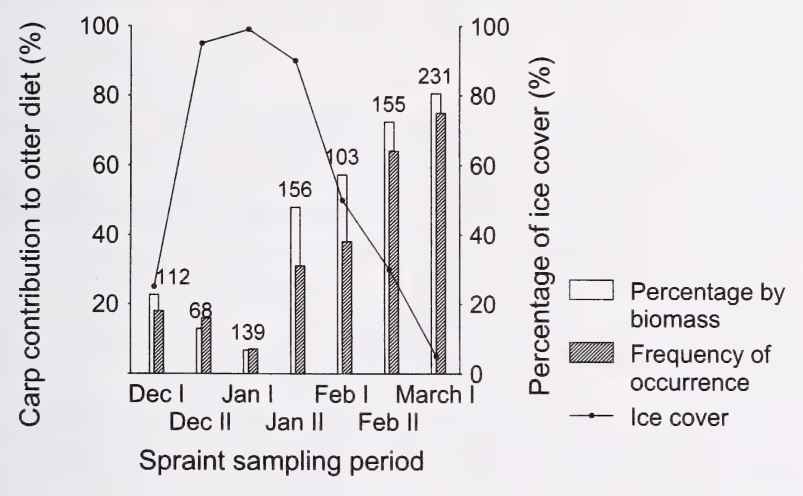


Fig. 3. Mean percentage of ice cover on the Tyśmienica fish-ponds to the total water surface of the ponds in November 1994–March 1995 and variation in the proportion of carp in terms of biomass and frequency of occurrence in otter diet (half-month samples). Numbers over columns are sample sizes.

found for wild fish ($r = 0.57$, $p > 0.18$ and $r = 0.75$, $p > 0.05$, respectively). After exclusion of the data from December–January, the period after establishment of persistent ice cover, the correlations between farm fish abundance and its proportion in otter diet were stronger, but still not significant ($r = 0.61$, $n = 10$, $p > 0.06$ for both methods of diet quantification).

Monthly changes in the calorific value of otter food per weight unit were inversely correlated with fluctuations in the proportion of thiaminase-free prey ($r = -0.85$, $n = 12$, $p < 0.001$; Fig. 4). June–August was the period of the lowest calorific content of the otters' food (the calorific equivalent of an 'average' digested 1 g dropped below 3.0 kJ), while the proportion of thiaminase-free prey was highest then, ranging from 41.4 % to 55.7 % of the consumed biomass. The energetic intake per 'digested' prey weight unit was greatest in February–March and November, when it reached 3.4 kJg^{-1}. In these months the proportion of thiaminase-free prey was the lowest, ranging from 2.4 % to 4.4 %.

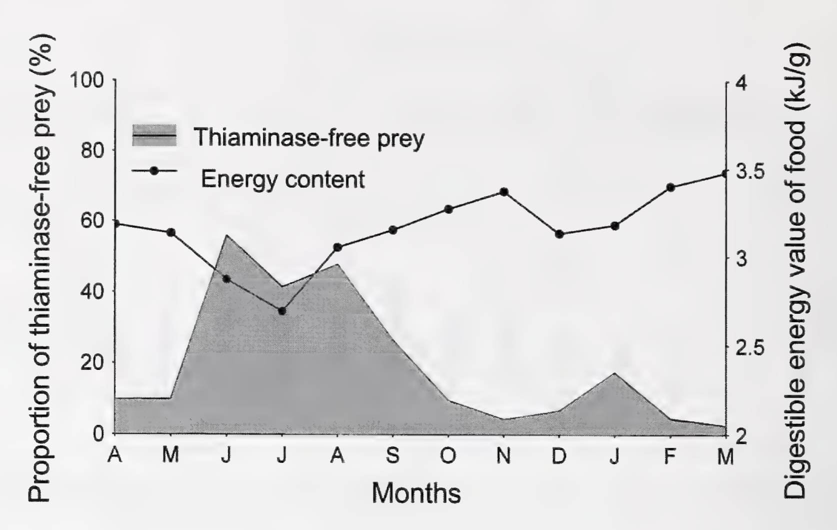


Fig. 4. Monthly variation in the digestible calorific value of otter 'average' food per weight unit and the proportions of thiaminase-free prey between April 1994 and March 1995.

The trophic niche breadth varied throughout the year, otters specializing most in summer (Levins' B falling from 5.0 in June to 3.6 in August) with another low in March (B = 4.9) while a wider range of items was eaten in December (B = 8.8) and January (B = 9.2). The total biomass of farm fish was not significantly correlated with diet breadth (r = 0.40, n = 12, p = 0.20).

Discussion

Assessing the proportion of prey categories in otter diet on the basis of faeces analysis must be regarded with caution. Carss and Parkinson (1996) and Jacobsen and Hansen (1996) pointed out some potential difficulties. The severest problem is the lack of statistical independence of the data following errors in estimation of the number of fish recorded per spraint and the number of droppings containing the remains of individual items. The applied recording procedure was chosen as a compromise between these demands. Identifying several different prey structures increases the likelihood of scoring a prey category (Cottrell et al. 1995), while the probability of recording a single item repeatedly, as may be common when using scales and vertebrae for quantifying prey number (Jacobsen and Hansen 1996), was minimized.

The present results show that cultured stocks constitute an important food resource for otters. However, since carp fraction in the otter diet declined with the increasing proportion of ice cover at ponds, the advantages of using the additional food resource in the period of an ecological 'bottleneck' were reduced. Presumably better access to water under ice was provided at rivers, while water inlets were occasionally the only unfrozen places in the ponds.

Farm fish was not taken in proportion to abundance. In April 41 % of the estimated otter diet consisted of carp, but only 26 % in August, despite the stock enhancement by a factor of 3.9. These considerations lack comparisons with the relative abundance of alternative prey, as neither good density estimates nor data on seasonal changes in otter ranges were available. Still, information provided by the local fishermen indicate that the

fish productivity of the Tyśmienica at its upper and middle reaches was poor and variations in wild fish abundance did not balance the changes in artificial food resources created by the vast pond complexes. This view gains some support from the fact that wild fish prey was markedly smaller than carps retrieved from spraints.

A series of carp vulnerability periods related to fish culture regime may be responsible for these seasonal disproportions. Predation at carp farms may increase during stock translocations, as cultured fishes are more vulnerable when under stress associated with transport (Olla et al. 1994). Fishes are also left unprotected due to lowering the water table during the few days of drawing down the ponds at harvests or restocking. In the study area these operations took place in March–April and September–October, and the proportion of carp in otter diet was relatively high in these months. Bad condition of carp after wintering may contribute to the peak of its exploitation in February–March.

Another possible reason for the shifts in carp use by otters is meeting of nutrient and energy requirements at different seasons. Even 20 % carp proportion in the diet can evolve clinical signs of thiamine deficiency in river otters *Lutra canadensis* after a long period (Aulerich et al. 1995). Consumption of thiaminase-containing food by Tyśmienica otters exceeded the above value by far throughout the year. Seasonal changes in the use of energy-rich prey coincided with inverse shifts in consumption of nutritionally valuable (thiaminase-free) food. In summer water temperatures are relatively high and some thiaminase-free prey types become available, whereas otters face hardship in winter as food requirements increase with decreasing water temperature (Kruuk 1995) and fish accessibility is restricted by ice cover. Shifts in prey choice, governed by a combined effect of seasonal food availability and its nutritional value, result in a balanced diet when it is averaged over long periods, but not in particular feeding periods (Westoby 1978). Although otters fed raw carp reject this food after a few days (S. Sikora, pers. comm.), clinical symptoms of thiamine defficiency in captive animals are considerably delayed in time, dependent on the degree of thiamine deprivation and fat content in the diet (Geraci 1974; Aulerich et al. 1995). Thus, under natural conditions switching to foods higher in thiamine may occur at longer intervals and thus produce a seasonal pattern. Still, spraint analysis allows no conclusions on the feeding behaviour of individual otters.

Despite the presence of densely stocked ponds, a partial shift to non-fish food was apparent in summer. The same predation pattern was stated on the basis of a relatively small spraint sample (n = 74) in the study area a year later, in June–July 1995. In July 1995 crayfish constituted over half of the estimated otter diet by weight (J. Kloskowski, unpubl.). Similar dietary shifts were demonstrated in other eutrophic habitats of temperate Europe (Erlinge 1967; Wise et al. 1981) and interpreted as response to changes in fish dispersion and motility. However, carp stocks were regulated by transfers independent of natural seasonal population dynamics. Dispersion in densely stocked ponds was restricted. Moreover, in summer many carps were observed being torpid close to the water surface, probably due to temporal oxygen drops and were an easy prey for otters. By contrast, crayfish was rare in the canalised and polluted waterflows of the region (Radwan and Girsztowtt 1994). In addition to the mentioned possible nutritional benefits, crayfish importance in the otter summer diet may be attributed to its increased activity in this period (Erlinge 1967). Preference for some alternative prey may have important implications for integrative management of aquatic habitats adjoining the fish farms, but its reasons have to be clearly determined.

More information is needed on diet composition at individual levels and long-term numerical responses of otters to changes in prey availability in conditions of patchily distributed monocultured fish supply. Considering the magnitude of cyprinid culture in central and eastern Europe and thriving otter populations in some parts of this region

(Brzeziński et al. 1996), further progress to elucide the factors influencing otter depredation of farm stocks may contribute to mitigation of large scale conflicts with aquacultural policy.

Acknowledgements

I gratefully acknowledge Ken Ishii for assistance in both the field and laboratory, the managers E. Łagowski and A. Gajda for the permission to work on the fish-farms and the information on fish stocks, and J. Ignatowicz for his help in analysing the data on fish supply.

Zusammenfassung

Beuteerwerb des Fischotters Lutra lutra in von Weißfischen dominierten Habitaten

Die Nahrung des Fischotters in einem Teichgebiet in Südostpolen wurde quantitativ untersucht, indem insgesamt 2048 Losungen, zweimal monatlich parallel zum alljährlichen Nutzungsmuster einer Karpfenzucht gesammelt und analysiert wurden. Die Zusammensetzung der Nahrung wurde mit Daten über den Fischbesatz verglichen. Die Präsenz der Karpfenbestände beinflußte die Zusammensetzung der Nahrung mit Karpfen als dem wichtigsten Bestandteil. Der Biomasseanteil von Karpfen an der Gesamtnahrung variierte von 15.7 % im Juni bis 78.0 % im März. Die Änderungen des Angebotes an Karpfen konnten die jährliche Variation der Prädation nicht erklären. Die für die jahreszeitlichen Verlagerungen in der Ressourcennutzung verantwortlichen Faktoren werden diskutiert.

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Z. Säugetierkunde **64** (1999) 210–219

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Contributions to the karyology and taxonomy of the genus *Spalax* Güldenstaedt, 1770 (Mammalia: Rodentia) in Turkey

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Receipt of Ms. 08. 02. 1999
Acceptance of Ms. 20. 04. 1999

Abstract

The karyotypes of 17 specimens in 10 localities belonging to *Spalax leucodon* (Nordmann, 1840), and 2 specimens of *Spalax ehrenbergi* Nehring, 1898 from Kilis in Turkey were analysed. It was determined that *S. leucodon* has 2n = 36 and NF = 70 in the Bayındır population; 2n = 60, NF = 82 and NFa = 78 in Ankara (centrum, 15 km N, and 35 km S), Afyon 10 km E and Afyon 95 km SW populations; 2n = 60, NF = 84 and NFa = 80 in the Burdur (centrum and 10 km W) population, and 2n = 60, NF = 76 and NFa = 72 in the Akşehir 10 km SE population. *S. ehrenbergi* from 15 km E of Kilis has also 2n = 52, NF = 74 and NFa = 70.

According to these karyological findings the diploid chromosome number of the Bayındır population, and the NF and NFa values of Burdur, Akşehir, and Kilis populations are new for the genus *Spalax* in Turkey.

Key words: *Spalax leucodon, Spalax ehrenbergi*, karyology, taxonomy, Turkey

Introduction

The subterranean mole rats belonging to the family Spalacidae are distributed throughout southeastern Europe, Asia Minor, Caucasus, Transcaucasus, Ukraine, Armenia, Syria, Palestine, Iraq, Israel, Jordan, and northeastern Africa (Ognev 1947; Ondrias 1966; Lay and Nadler 1972; Corbet 1978; Giaga et al. 1982; Nevo 1991: Harrison and Bates 1991). To date, over 40 chromosomal forms of *Spalax* have been reported in the literature from these areas.

According to the most recent morphological studies there are two species (*S. leucodon* and *S. ehrenbergi*) and nine subspecies (*S. l. nehringi, S. l. armeniacus, S. l. cilicicus, S. l. anatolicus, S. l. turcicus, S. l. tuncelicus, S. e. intermedius, S. e. kirgisorum,* and *S. e. nevoi*) of blind mole rats in Turkey (Kivanç 1988; Coşkun 1996 a, b). However, the results from karyological studies revealed nine karyological forms of *S. leucodon* (2n = 38, 40, 50, 52, 54, 56, 58, 60, and 62) and four karyological forms of *S. ehrenbergi* (2n = 52, 54, 56, and 58) in Turkey, and the number of chromosome arms (NF) for *S. leucodon* and *S. ehrenbergi* varied from 70 to 82 and from 72 to 90, respectively (Soldatovic and Savic 1978; Savic and Soldatovic 1979; Yüksel 1984; Gülkaç and Yüksel 1989; Yüksel and Gülkaç 1992, 1995; Nevo et al. 1994, 1995; Ivanitskaya et al. 1997; Sözen and Kivanç 1998 a, b). Nevo et al. (1994, 1995) stated that each of the chromosomal forms is a separate biological species. They examined the populations using Nei's genetic distance between populations obtained by allozyme electrophoresis and claimed that

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some populations having identical diploid chromosome numbers are different biological species, presumably representing about 20 such species in Turkey. They also showed that in Turkish *Spalax*, speciation and adaptation positively correlate with aridity stress and climatic unpredictability. 2n values and heterozygosity, *H*, increase toward the ecologically harsh, arid, and climatically unpredictable and geologically young central Anatolian Plateau from the west, north, south, and east (Nevo et al. 1994, 1995). The number of biological species determined by a combination of chromosome number, genetic distances, and ecogeography of *Spalax* is tend to increase by new studies (Sözen and Kivanç 1998a, b).

The results of these studies demonstrate the necessity to reexamine the species and subspecies specified morphologically, and to determine the borders of chromosomal forms. The aim of this present study is to give the karyologic characteristics of the blind mole rats collected from given localities, and thereby to contribute to karyology, taxonomy, and speciation of the genus *Spalax* in Turkey.

Material and methods

The karyotypes of 1 female specimen from Bayındır (İzmir), 6 specimens (5 males, 1 female) from three localities in Ankara, 2 male specimens from 10 km SW of Afyon, 1 female specimen from 95 km SW of Afyon, 5 specimens (2 males, 3 females) from two localities in Burdur, and one female specimen from 10 km SW of Akşehir belonging to *Spalax leucodon* (Nordmann, 1840), and 2 male specimens of *Spalax ehrenbergi* Nehring, 1898 from 15 km E of Kilis in Turkey were analysed (Fig. 1, Tab. 1). Bayındır, Ankara, Afyon, Burdur, and Akşehir specimens were determined as *S. leucodon*, and specimens from Kilis as *S. ehrenbergi*. Karyotypes were prepared from bone marrow according to Ford and Hamerton (1956), and about 25–30 metaphase cells, which were well-stained, and whose chromosomes were separate and distinct, were examined from each animal. The diploid number of chromosomes (2n), the number of autosomal arms (NFa), and the total number of chromosomal arms (NF) were determined together with metacentric (m), acrocentric (a), subtelocentric (st), and submetacentric (sm) according to centromere positions, and sex chromosomes. The karyotype preparations and the animals examined were deposited in Department of Biology, Faculty of Science, University of Ankara.

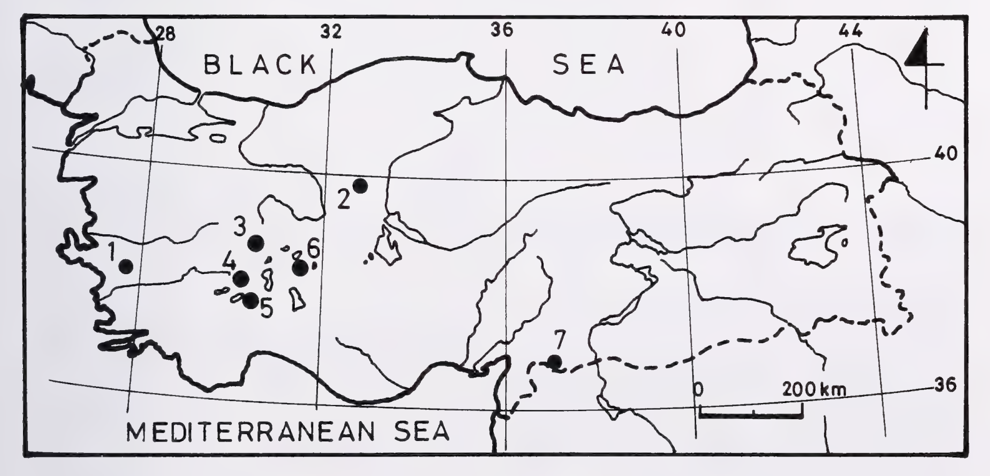


Fig. 1. Map of Turkey with localities of the analysed populations. 1. Bayındır, 2. Ankara, 3. Afyon 10 km W, 4. Afyon 95 km SW, 5. Burdur, 6. Akşehir, 7. Kilis 15 km E.

Table 1. The location and the number of animals examined.

Spalax leucodon (Nordmann, 1840)			
Locality	Male	Female	Total
Bayındır	–	1	1
Ankara (Centrum)	1	1	2
Ankara 15 km N	–	1	1
Ankara 35 km S	3	–	3
Afyon 10 km E	2	–	2
Afyon 95 km SW	–	1	1
Burdur 5 km S	2	2	4
Burdur 10 km W	–	1	1
Akşehir 10 km SE	1	1	2
Spalax ehrenbergi Nehring, 1898			
Kilis 15 km E	2	–	2

Results

Spalax leucodon (Nordmann, 1840)

Bayındır (Izmir) population: The karyotype of one female specimen from Bayındır in western Turkey was analysed. According to this analysis the Bayındır population has a karyotype of 2 n = 36, NF = 70. The karyotype contains 5 pairs of metacentric, 10 pairs of submetacentric, 2 pairs of subtelocentric, and 1 pair of acrocentric chromosomes (Fig. 2 a).

Ankara (centrum, 15 km N, and 35 km S), Afyon (10 km E, Afyon 95 km SW) populations: We determined the karyotypes of these five populations as 2 n = 60, NF = 82, and NFa = 78. The X chromosome is a medium-sized submetacentric, and the Y chromosome is the smallest subtelocentric. The autosomal set contains 10 pairs of subtelocentric, and 19 pairs of acrocentric chromosomes (Fig. 2 b).

Burdur 5 km S and 10 km W populations: The karyotype of Burdur populations has 2 n = 60, NF = 84, and NFa = 80. The X chromosome is a medium-sized submetacentric, and the Y chromosome is the smallest subtelocentric. The autosomal set contains 11 pairs of subtelocentric and 18 pairs of acrocentric (Fig. 3 a).

Akşehir 19 km SE population: The Akşehir populations have a karyotype of 2 n = 60, NF = 76, and NFa = 72. The X chromosome is a medium-size submetacentric, and the Y chromosome is the smallest subtelocentric. The autosomal set contains 7 pairs of subtelocentric and 22 pairs of acrocentric chromosoes (Fig. 3 b).

Spalax ehrenbergi Nehring, 1898

Kilis 15 km E population: The karyotype of 2 male specimens from 15 km east of Kilis was examined. The karyotype contains of 2 n = 52 chromosomes, NF = 74, and NFa = 70. The X chromosome is a medium sized submetacentric and the Y chromosome is acrocentric. The autosomal set of this population has 4 pairs of metacentric, 3 pairs of submetacentric, 3 pairs of submetacentric, and 15 pairs of acrocentric chromosomes (Fig. 4).

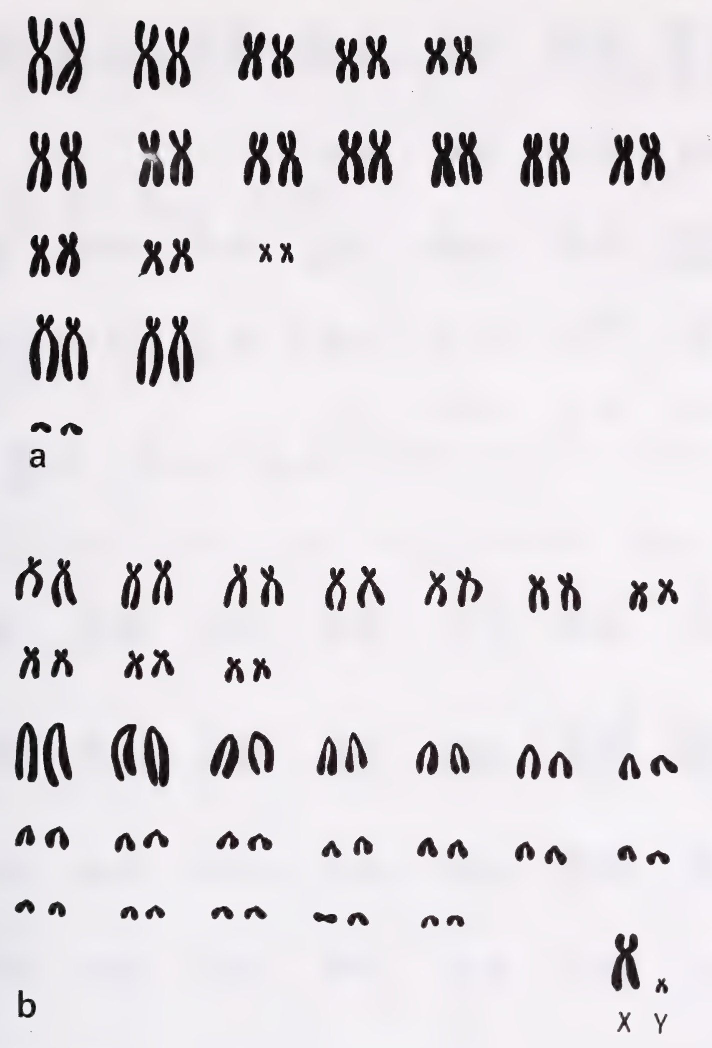


Fig. 2. The karyotype of a female *Spalax leucodon* from Bayındır (a), a male from Ankara (b).

Discussion

The first karyological analysis of the blind mole rat *Spalax leucodon* in Turkey was introduced by Soldatovic and Savic (1978) from the Thrace region of Turkey (Çorlu and Karaevli), and corresponding investigations on the Asian part of Turkey (Havran and Selçuk) were performed by the same authors (Savic and Soldatovic 1979). Later, new karyotypes were determined from the territory of Malatya by Yüksel (1984); from Malatya, Yazıhan, and Arguvan by Gülkaç and Yüksel (1989); from Kırşehir, Nevşehir, Kayseri, and Yozgat by Yüksel and Gülkaç (1995); from Balıkesir, İzmir, Beyşehir, Aydın, Erzurum, Sarıkamış, Bolu, Bingöl, Denizli, Pınarbaşı, Malatya, Kütahya, Afyon, Konya, Sivas, Ankara, Kayseri, Havza, and Suşehri by Nevo et al. (1994); from Malatya by Ivanitskaya et al. (1997); from Sebil, Gülek by Sözen and Kıvanç (1998 a), and from Madenköy by Sözen and Kıvanç (1998 b).

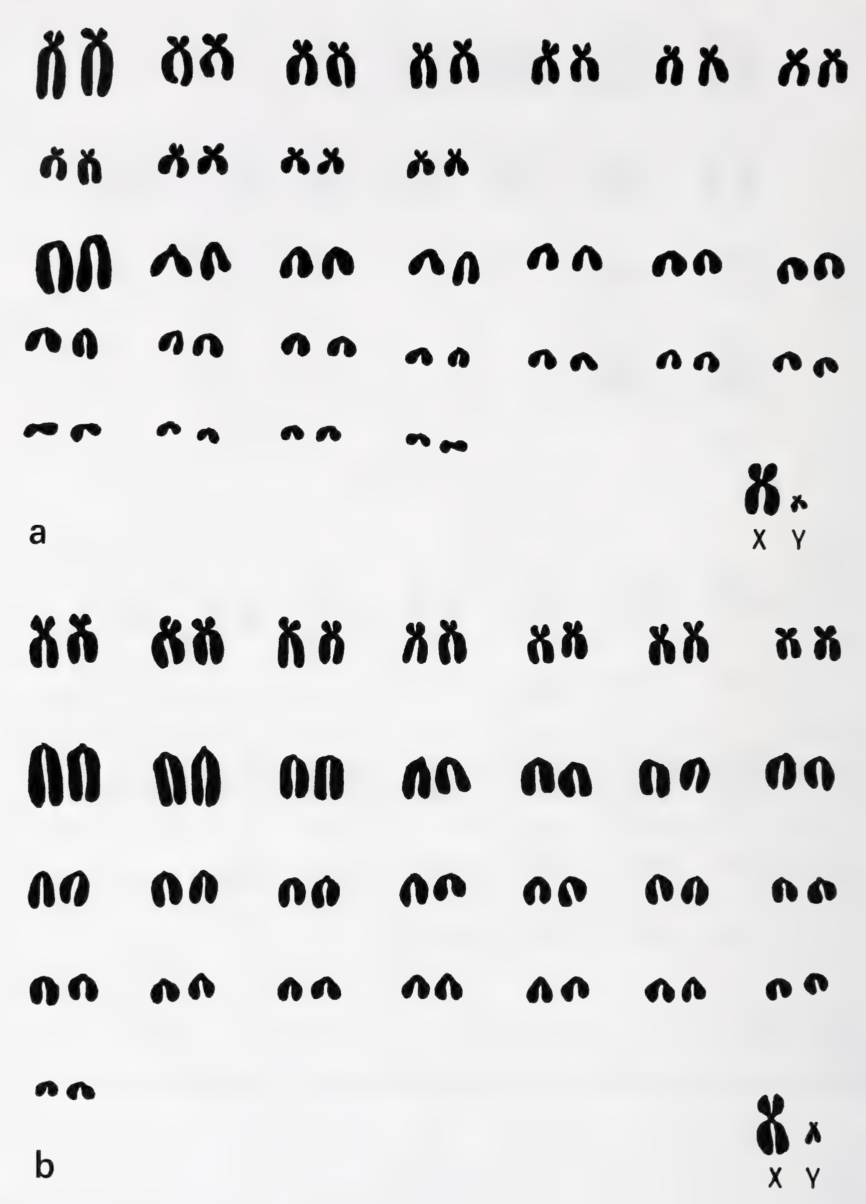


Fig. 3. The karyotype of a female *Spalax leucodon* from Burdur (a), a male from Akşehir (b).

The karyotype of *S. ehrenbergi* was first given by YÜKSEL (1984) from Elazığ, then by YÜKSEL and GÜLKAÇ (1992) from Adıyaman, Hilvan, Suruç, and Gaziantep; by NEVO et al. (1994) from Diyarbakır, Urfa, Gaziantep, and Tarsus; by IVANITSKAYA et al. (1997) from Tarsus, Gaziantep, Elazığ and Urfa (Tab. 2).

According to these studies the diploid karyotypes of *Spalax leucodon* in Turkey vary between 2n = 38 and 62, NF = 70 and 82, and NFa = 68 and 78. *Spalax ehrenbergi* also has a karyotype varying between 2n = 52 and 58, NF = 72 and 90, and NFa = 68 and 86.

The karyotype of *S. leucodon* determined in this study from Bayındír, 2n = 36, NF = 70 is a first record for *S. leucodon* populations in Turkey, and also for all *Spalax* po-



Fig. 4. The karyotype of a male *Spalax ehrenbergi* from Kilis.

pulations. This karyotype pattern is smaller than in all the other populations in the distribution area of the Spalacidae. The karyotypes given by Savic and Soldatovic (1979) from Havran and Selçuk, and by Nevo et al. (1994, 1995) from Balıkesir and İzmir are close to this karyotype.

The diploid karyotypes of Ankara and Afyon populations determined here are identical with the Arguvan population given by Gülkaç and Yüksel (1989) on the basis of chromosomal arm size and the chromosome morphology. These populations have 2n = 60, NF = 82 and NFa = 78 containing 10 pairs of subtelocentric, 19 pairs of acrocentric autosomal chromomes, and a submetacentric X chromosome. In contrast to our findings, Nevo et al. (1994, 1995) specified the diploid chromosome number as being 2n = 62 from 30 km S of Ankara and 35 km E of Afyon. This shows that two different chromosomal forms of *Spalax* are distributed in Ankara, and Afyon provinces.

The diploid karyotype of Afyon, Ankara, Burdur, and Akşehir determined here is 2n = 60, but the NF and NFa values are different (Tab. 2). NF = 84, NFa = 80 of the Burdur population, and NF = 76, NFa = 72 of the Beyşehir population represents the first records for Turkish *Spalax*.

The diploid karyotype of *S. ehrenbergi* given by us is similar to the diploid chromosome number but different, on the basis of chromosomal arm size and the chromosome morphology, from karyotypes given by Yüksel (1984) from Elazığ by Yüksel and Gülkaç (1992) from Adıyaman and Hilvan, by Nevo et al. (1994, 1995) from Diyarbakır and Urfa, and by Ivanitskaya et al. (1997) from Birecik, Siverek, Diyarbakır and Elazığ, and from Urfa (Tab. 2).

Table 2. Chromosomal records of *Spalax leucodon* (Nordmann, 1840) and *Spalax ehrenbergi* Nehring, 1898 from Turkey.
*m: metacentric, sm: submetacentric, st: subtelocentric, a: acrocentric

Spalax leucodon (Nordmann, 1840)						
Locality	2n	NF	NFa	X	Y	Reference
Çorlu and Karaevli (in Thrace)	56	78	74	sm*	a*	SOLDATOVIC and SAVIC (1978)
Havran and Selçuk	38	74	70	st*	a	SAVIC and SOLDATOVIC (1979)
Malatya	60	78	74	sm	a	IVANITSKAYA et al. (1997)
Malatya	60	80	76	sm	st	YÜKSEL (1984)
Malatya and Yazıhan	60	80	76	sm	st	GÜLKAÇ and YÜKSEL (1989)
Arguvan	60	82	78	sm	–	GÜLKAÇ and YÜKSEL (1989)
Kırşehir, Nevşehir and Kayseri	60	80	76	sm	st	YÜKSEL and GÜLKAÇ (1995)
Yozgat	54	74	70	sm	st	YÜKSEL and GÜLKAÇ (1995)
Balıkesir and İzmir	38	74	70	st	a	NEVO et al. (1994, 1995)
Beyşehir	40	72	68	sm	–	NEVO et al. (1994, 1995)
Aydın, Erzurum	50	–	–	–	–	NEVO et al. (1994, 1995)
Sarıkamış	50	70	68	sm	–	NEVO et al. (1994, 1995)
Bolu and Bingöl	54	–	–	–	–	NEVO et al. (1994, 1995)
Denizli, Pınarbaşı	60	–	–	–	–	NEVO et al. (1994, 1995)
Malatya	60	78	74	sm	a	NEVO et al. (1994, 1995)
Kütahya, Afyon, Konya, Sivas, Ankara, Kayseri, Havza, Suşehri	62	–	–	–	–	NEVO et al. (1994, 1995)
Gülek	56	72	68	m	a	SÖZEN and KIVANÇ (1998 a)
Sebil	52	72	68	sm	a	SÖZEN and KIVANÇ (1998 a)
Madenköy	58	72	68	sm	a	SÖZEN and KIVANÇ (1998 b)
Bayındır	36	70	–	–	–	This study
Ankara centrum, 15 km N, and 35 km S	60	82	78	sm	st	This study
Afyon 95 km SW and 10 km E	60	82	78	sm	st	This study
Burdur 5 km S and 10 km W	60	84	80	sm	st	This study
Akşehir 10 km SE	60	76	72	sm	st	This study
Spalax ehrenbergi Nehring, 1898						
Locality	2n	NF	NFa	X	Y	Reference
Elazığ	52	76	72	sm	st	YÜKSEL (1984)
Adıyaman and Hilvan	52	76	72	m*	st	YÜKSEL and GÜLKAÇ (1992)
Suruç	54	76	72	m	st	YÜKSEL and GÜLKAÇ (1992)
Gaziantep	56	90	86	m	st	YÜKSEL and GÜLKAÇ (1992)
Diyarbakır and Urfa	52	76	72	–	–	NEVO et al. (1994, 1995)
Gaziantep	58	82	78	–	–	NEVO et al. (1994, 1995)
Tarsus	56	72	68	–	–	NEVO et al. (1994, 1995)
Tarsus	56	72	68	m	–	IVANITSKAYA et al. (1997)
Gaziantep	56	82	78	sm	–	IVANITSKAYA et al. (1997)
Birecik, Siverek, Diyarbakır, Elazığ	52	76	72	sm	–	IVANITSKAYA et al. (1997)
Urfa	52	80	76	sm	–	IVANITSKAYA et al. (1997)
Kilis 15 km E	52	74	70	sm	a	This study

The sex chromosomes are variable in both *S. leucodon* and *S. ehrenbergi*. In most populations of *S. leucodon* in Turkey, the X chromosome was described as being submetacentric (SOLDATOVIC and SAVIC 1978; YÜKSEL 1984; GÜLKAÇ and YÜKSEL 1989; YÜKSEL and GÜLKAÇ 1995; IVANITSKAYA et al. 1997; SÖZEN and KIVANÇ 1998 a, b), subtelocentric in two populations in western Turkey (SAVIC and SOLDATOVIC 1979), and metacentric only in the Gülek population (SÖZEN and KIVANÇ 1998 a). The Y chromosome is acrocentric (SOLDA-

TOVIC and SAVIC 1978; SAVIC and SOLDATOVIC 1979; SÖZEN and KIVANÇ 1998 a, b), or subtelocentric (YÜKSEL and GÜLKAÇ 1995; YÜKSEL 1984; GÜLKAÇ and YÜKSEL 1989; SÖZEN and KIVANÇ 1998 a, b). We found that the X chromosome is also submetacentric in all populations studied, and that the Y chromosome is subtelocentric. In *S. ehrenbergi* populations, the X chromosome is submetacentric (YÜKSEL 1984; IVANITSKAYA et al. 1997) or metacentric (YÜKSEL and GÜLKAÇ 1992; IVANITSKAYA et al. 1997), and the Y chromosome is subtelocentric (YÜKSEL 1984; YÜKSEL and GÜLKAÇ 1992; IVANITSKAYA et al. 1997). We determined that the X chromosome is submetacentric, and the Y chromosome is acrocentric in the Kilis population.

The subterranean Spalacidae probably originated from a muroid-cricetoid stock in Asia Minor or vicinity, during Oligocene times, about 30–40 mya, and radiated adaptively underground in the Balkans, steppic Russia and Middle East, extending into North Africa (SAVIC and NEVO 1990).

The major important evolutionary feature was karyotypic evolution, mainly based on Robertsonian changes (SAVIC and NEVO 1990). More than 40 karyotypes (2 n = 38–62, NF = 72–124) occur across the eastern Mediterranean range of the family. Most karyotypes represent biospecies adapted to their different ecologies at multiple organizational levels. Three major chromosomal trends (2 n = 38–62) occur across the entire Eurasian and east Mediterranean range of Spalacidae, all starting in Western Turkey. These involve: (1) the Near East and North Africa (2 n = 38 → 62); (2) the Balkans (2 n = 38 → 62), and (3) the Ukrainian and Russian steppes, 2 n = 38 → 62 (NEVO 1991; NEVO et al. 1995). This trend has also been revealed in Turkey itself supporting the idea of ecological speciation via chromosome speciation (NEVO et. al 1995). The chromosome number of *Spalax* tends to increase during adaptive radiation from humid areas toward the ecologically harsh, arid, and climatically unpredictable and geologically young central Anatolian Plateau from all directions (NEVO et al. 1994, 1995). The Bayındır population (2 n = 36, NF = 70) determined in this study is now acceptable to be the speciation center of Spalacidae. But this concept should be supported by new molecular and fosil findings.

NEVO et al. (1995) determined 10 karyotypes and probably more than 20 new species, based on karyotypes and genetic distances, to the two superspecies *leucodon* and *ehrenbergi*, in Turkey. Later SÖZEN and KIVANÇ (1998 a, b) determined three new karyotypes in the superspecies *leucodon*. In the present study, we have determined four extra karyologic forms for the two superspecies *leucodon* and *ehrenbergi*, one of them has a new 2 n value (Bayındır population), and three of them have new NF and NFa values (Burdur, Akşehire, and Kilis populations). These results bring the total number of karyological forms or biospecies of Turkish *Spalax* to approximately 30.

According to the findings mentioned above, the borders of the areas of all chromosomal forms described from Turkey are not definite because of the possibility of the existence of new localities and chromosomal forms. It will certainly be necessary to analyse greater numbers of populations of the blind mole rats to determine the borders of the areas of all the described chromosomal variations from Turkey and to find possible new karyological forms and thereby to explain precisely speciation, phylogeny, systematics, and the evolutionary history of Spalacidae in Turkey.

Zusammenfassung

Zur Karyologie und Taxonomie der Gattung Spalax Güldenstaedt, 1770 (Mammalia: Rodentia) in der Türkei

Die Karyotypen von 17 Individuen der Art *Spalax leucodon* (Nordmann, 1840) aus 10 Probengebieten in der Türkei sowie von 2 Individuen der Art *Spalax ehrenbergi* Nehring, 1898 aus Kilis, Türkei, wur-

den analysiert. *S. leucodon* zeigte 2 n = 36 und NF = 70 in Bayindir; 2 n = 60, NF = 82 und NFa = 78 in Ankara (Zentrum, 15 km N und 35 km S), Ayfon (10 km O und 95 km SW); 2 n = 60, NF = 84 und NFa = 80 in Budur (Zentrum und 10 km W) und 2 n = 60, NF = 76 und NFa = 72 in Akşehir (10 km SO). *S. ehrenbergi* aus Kilis (15 km O) zeigte 2 n = 52, NF = 74 und NFa = 70. Nach unseren karyologischen Ergebnissen weisen die diploide Chromosomenzahl von Individuen aus Bayindir sowie die NF und NFa bei Individuen aus Budur, Akşehir und Kilis bei der Gattung *Spalax* in der Türkei bisher nicht beobachtete Werte auf.

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Z. Säugetierkunde **64** (1999) 220–229
http://www.urbanfischer.de/journals/saeugetier


ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Karyotype relationship among four species of Spiny mice (*Acomys*, Rodentia)

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Receipt of Ms. 02. 11. 1998
Acceptance of Ms. 24. 03. 1999

Abstract

G-banded karyotypes of four species of the genus *Acomys* from different localities are described: *Acomys cahirinus* from Egypt, *A. cineraceus* from the Sudan, *A. dimidiatus* from Israel and *A. minous* from Crete. Diploid chromosome numbers vary considerably among these species, ranging from 2n = 36 to 2n = 50. The variation is due to Robertsonian fusions and/or fissions. We constructed a maximum parsimony tree using the common Robertsonian metacentrics as characters.

Key words: *Acomys*, karyotype, Robertsonian chromosome, phylogeny

Introduction

The genus *Acomys* (spiny mice) has a wide geographical distribution from South Africa to southwest Asia and as far north as Crete and Turkey. Preferring rocky habitats, *Acomys* displays a patchy distribution with many populations isolated on cliffs and rocky hills (VOLOBOUEV et al. 1991). Currently, 52 taxa are assigned to the genus *Acomys*. They have been assembled into a variety of subgenera, species groups, and species (BATES 1994). Due to the absence of unequivocal diagnostic markers, the taxonomic classification changed several times. The proposed number of species ranges from 14 (MUSSER and CARLETON 1993) to 38 (ELLERMANN 1941). We follow the classification of DENYS et al. (1994) who gave diagnoses based on skull morphology, dental pattern, allozyme patterns, and karyotypes.

VOLOBOUEV et al. (1991, 1996 a, b) applied cytotaxonomy to clarify the confusing systematics of this group. Karyotypes display a wide variation among species. Diploid chromosome numbers from 2n = 36 to 2n = 68 have been found. The variation is presumed to be mainly due to centric fusion and fission events (Robertsonian translocations).

In this study we describe the G-band karyotypes of four species of *Acomys* and draw phylogenetic conclusions from the presence of common Robertsonian (Rb) chromosomes.

Material and methods

Animals

Our specimen of *A. minous* (Bate, 1905) was from Crete. Specimens from *A. cahirinus* (Desmarest, 1819) were kindly provided by the Zoological Garden of Cairo. Animals originally derived from Abu Rawash (Egypt) had yellow coat colour, those from Kardasa (Egypt) were grey. *A. cineraceus*

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(Fitzinger and Heuglin, 1866) was from two sources: the Blue Nile province (Sudan) and the province of Kordofan (Sudan). The Kordofan specimens were kindly provided by the late Dr. Jochen Niethammer (Bonn). *A. dimidiatus* (Cretzschmar, 1826) was trapped in Jerusalem by the late Dr. Alfred Gropp (Lübeck) and by Dr. Jacob Wahrman (Jerusalem). The *A. minous* (♀)×*A. dimidiatus* (♂) hybrid had been bred and kindly supplied by Dr. Jacob Wahrmann.

Mitotic chromosomes

Metaphase chromosomes were G-banded according to Seabright (1971). At least 10 metaphases from each species were analysed.

Meiotic chromosomes

The ovaries of the hybrid animal were dissected out and placed into cell culture medium (TC199). Oocytes were released by puncturing mature follicles with fine needles. The oocytes were collected and transferred into a petri dish with fetal calf serum. They were incubated at 36 °C for about six hours, then in 1 % Na-citrate for about 15 minutes. After transfer to clean slides in a drop of hypotonic solution, spreading and fixation were achieved by dropping methanol : acetic acid (3 : 1) onto the cells. Chromosomes were stained with orcein.

Results and discussion

Karyotypes

The *A. cahirinus* specimens had 18 chromosome pairs (2n = 36), 16 of which were metacentric (Fig. 1). Only the smallest pair of autosomes (no. 17) was acrocentric. Karyotypes of individuals from Abu Rawash and Kardasa were identical. The karyotypes are in keeping with the R-band karyotype published by Volobouev (1996 b).

The *A. minous* complement consisted of 19 chromosome pairs (2n = 38). Of the autosome pairs, 15 were metacentric and three acrocentric (Fig. 2). According to Matthey (1963), the *A. minous* karyotype is polymorphic. It contains 14 pairs of metacentrics and either four or five pairs of acrocentric autosomes. Our *A. minous* karyotype may have been derived from the latter one by a Robertsonian fusion (or the latter one from our karyotype by a fission event).

A. cineraceus from the Blue Nile province (Sudan) was polymorphic. The chromosome complement consisted of 25 pairs (2n = 50) with nine metacentric ones (Fig. 3) or of 24 chromosome pairs (2n = 48), among which ten were metacentric. One of the latter metacentrics was related to the acrocentric chromosomes no. 16 and no. 18 (indicated with asterisks in Fig. 3) by a Robertsonian fission/fusion event. The chromosome complement of specimen from Kordofan was identical to the 2n = 48 karyotype.

The *A. dimidiatus* specimen from Israel had 19 chromosome pairs (2n = 38), 16 of which were metacentric (Fig. 4). The same number of chromosomes was found in *A. cf. dimidiatus* from Saudi Arabia by Volobouev et al. (1991).

The sex chromosomes of all four *Acomys* species were acrocentric.

Common Robertsonian metacentrics

To investigate the phylogenetic relationship, we compared the mitotic karyotypes of the four species. Single arm comparisons proved unsatisfactory as the low number of bands did not allow safe identification. We were in a better position with whole Robertsonian metacentrics (Rbs). They afforded the combined banding pattern of the two arms and the

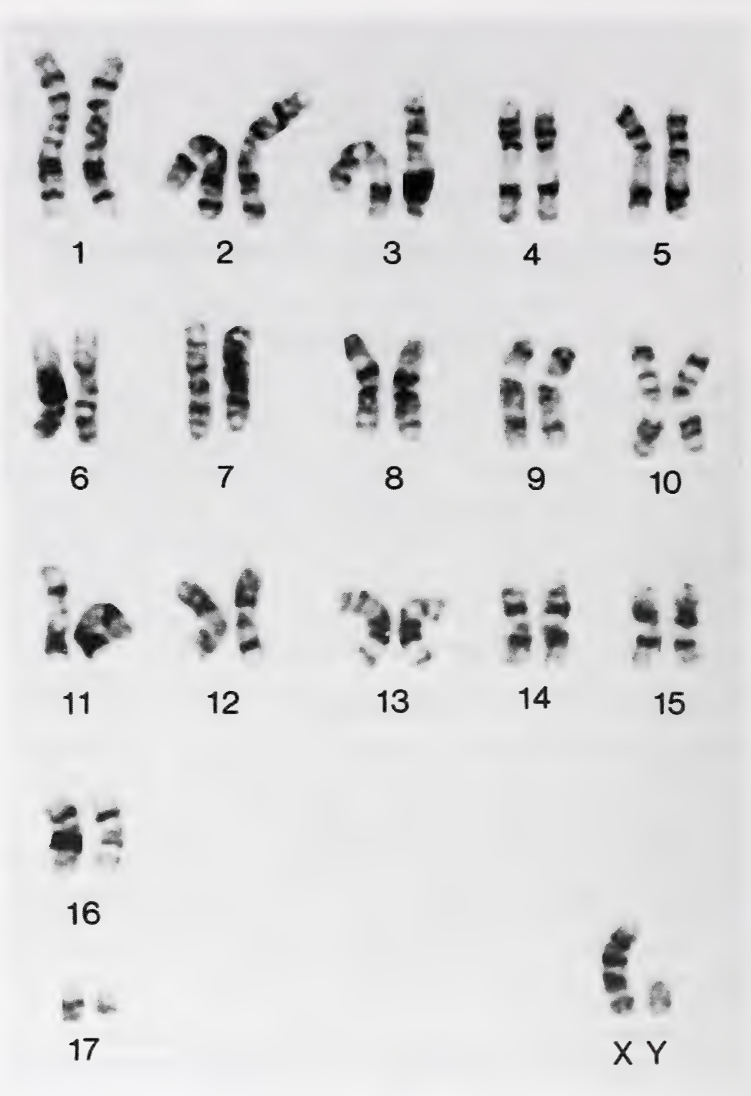


Fig. 1. G-band karyotype of *Acomys cahirinus* ♂ from Abu Rawash. Chromosomes were arranged according to size within each of three groups, metacentric autosomes, acrocentric autosomes and sex chromosomes.

centromere position as characters for identification. We focussed, therefore, on the recognition of common Rbs among the four species.

Several Rbs common to two or more species have been identified (Tab. 1). The karyotypes of *A. cahirinus* and *A. minous* had 15 Rbs in common (Tab. 1: A–O). The arms of *A. cahirinus* Rb chromosome no. 1 had their counterparts in the *A. minous* acrocentrics no. 16 and no. 17. Three Rbs (D, L, O; Fig. 5, Tab. 1) from *A. cahirinus* were found in *A. minous* and *A. cineraceus*, another Rb (G; Fig. 5, Tab. 1) in *A. cahirinus*, *A. minous*, and *A. dimidiatus*.

Our identification of one common Rb in *A. minous* and *A. dimidiatus* was supported by diakinesis figures from an *A. minous* (♀) × *A. dimidiatus* (♂) hybrid. The ooyctes of



Fig. 2. G-band karyotype of *A. minous* ♂. Arrangement of chromosomes as in Fig. 1.

the hybrid displayed three bivalents and two multivalent chains (Fig. 6). Most probably, the smallest bivalent (Fig. 6, arrowhead) consists of the paired acrocentrics no. 18 from *A. minous* and no. 18 from *A. dimidiatus* while the larger ring bivalents (Fig. 6, arrows) are the X chromosome bivalent and the bivalent of the only common Rb (G, Tab. 1). The two multivalent chains comprise all remaining chromosomes. Such synaptic chains are well known from hybrids between different Rb chromosome races, e. g., from *Mus musculus* (Johannisson and Winking 1994). They are characteristic for pairing of Rbs with alternating arm composition. The two chains in the *Acomys* hybrid are, therefore, evidence for the presence of Rbs with non-homologous arm composition in the parent species. The chains are terminated at their ends by 3 acrocentrics (two from *A. minous* and one from *A. dimidiatus*) and one small *A. dimidiatus* metacentric chromosome which, according to Volobouev et al. (1996 a) originated from an acrocentric one by an inversion. Hence, the pairing figures are fully accounted for.

Matthey (1963) published a meiosis figure from a hybrid which was designated *A. cahirinus* (♀) × *A. minous* (♂) but which according to the classification of Al-Saleh (1988) is to be considered an *A. dimidiatus* (♀) × *A. minous* (♂) hybrid. Thus, this is in



Fig. 3. G-band karyotype of *A. cineraceus* ♂ from Blue Nile. Arrangement of chromosomes as in Fig. 1.

fact the reciprocal hybrid to the one described by us and it confirms the conclusions drawn. The only apparent difference is the formation of three instead of two multivalent chains. This agrees with the presence of five instead of three acrocentric autosomes in the *A. minous* parent karyotype.

In contrast to us, Volobouev et al. (1996 b) did not find a common Rb in the complements of *A. cahirinus* and *A. dimidiatus*. This may have been due to a difference between populations. The animal investigated by Volobouev et al. (1996 b) came from Saudi Arabia, while our *A. dimidiatus* specimen was from Israel.

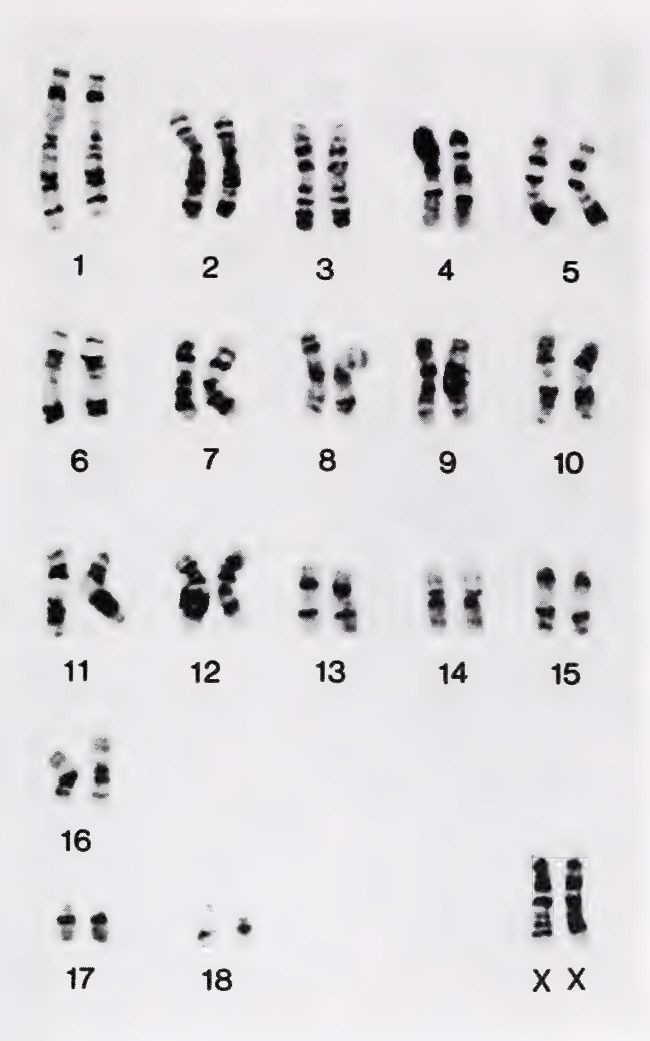


Fig. 4. G-band karyotype of *A. dimidiatus* ♀. Arrangement of chromosomes as in Fig. 1.

Karyotype evolution

The presence of common Rbs (Tab. 1) was translated to a maximum parsimony tree (Fig. 7). The only inconsistant character with respect to the tree topology is Rb G.

This Rb was either present at the root of the tree and lost in the *A. cineraceus* branch (Fig. 7 a) or it was independently created by fusion in the *A. dimidiatus* and in the *A. cahirinus/A. minous* branch (Fig. 7 b). We favour the interpretation represented in figure 7 a. The presence of a high number of chromosomes considered, the probability to create the same Rb in independent translocation events is low.

According to our dendrogram *A. cahirinus* and *A. minous* are the closest relatives among the four species. According to morphological parameters *A. minous* was treated as a separate species which belongs to the *A. cahirinus-A. dimidiatus* group (Corbet and Hill 1991; Denys et al. 1994; Dieterlen 1978). Morphologically *A. cahirinus* and

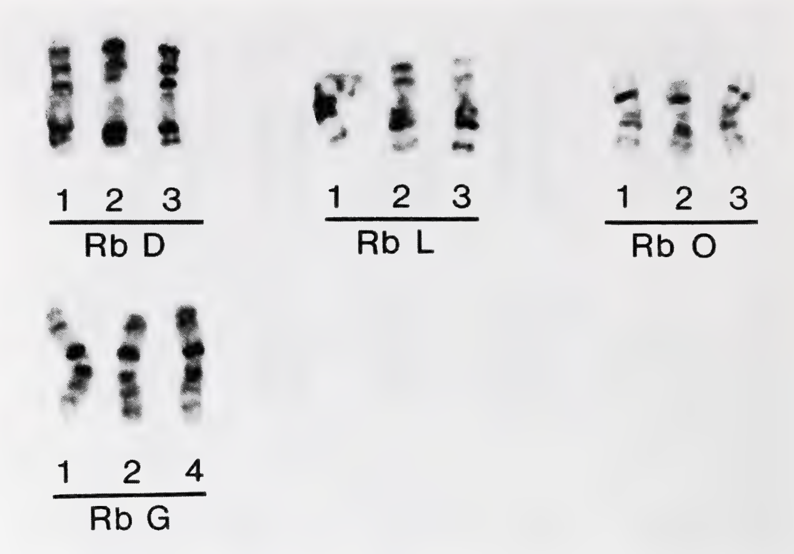


Fig. 5. Common Rb chromosomes in three *Acomys* species. Designation of Rbs according to table 1. Chromosomes from *A. cahirinus* (1), *A. minous* (2), *A. cineraceus* (3), and *A. dimidiatus* (4).

Table 1. Rb chromosomes common to at least two *Acomys* species (numbering of chromosomes according to figures 1–4).

A. cahirinus no.	*A. minous* no.	*A. cineraceus* no.	*A. dimidiatus* no.	Designation
2	1			A
3	2			B
4	3			C
5	4	3		D
6	5			E
7	6			F
8	7		9	G
9	8			H
10	9			I
11	10			J
12	11			K
13	12	7		L
14	13			M
15	14			N
16	15	9		O

A. dimidiatus appear to be the closest relatives, they are nearly indistinguishable (Volobouev et al. 1996b). The distance of *A. cahirinus* and *A. dimidiatus* is confirmed, however, by a comparison of satellite DNA sequences (Kunze et al. 1999).

The evolutionary history of the genus *Acomys* is not well documented, but the starting point appears to be tropical Africa with the oldest fossil records being about 7–8 my old (Denys et al. 1994). *Acomys* species with different Rbs were assumed by Volobouev et al. (1996a) to be derived from a common ancestor with a karyotye of 68–70 acrocentric chromosomes. Denys et al. (1994) assumed that this hypothetic common ancestor spread slowly over the continent and reached North Africa about 120 000 years ago and

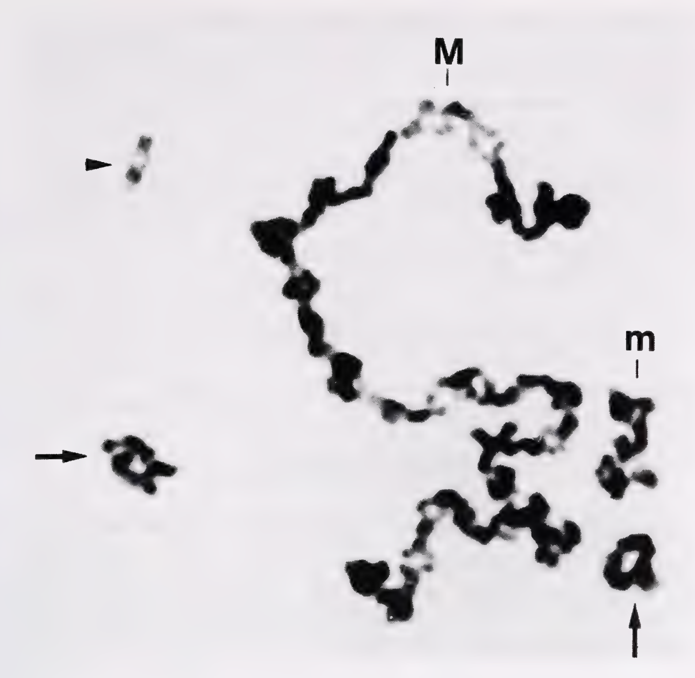


Fig. 6. Diakinesis figure of an *A. minous* (♀) × *A. dimidiatus* (♂) female hybrid. Arrowhead: bivalent of two acrocentric autosomes; arrows: ring bivalents of X/X and Rb G; m: short multivalent chain; M: long multivalent chain.

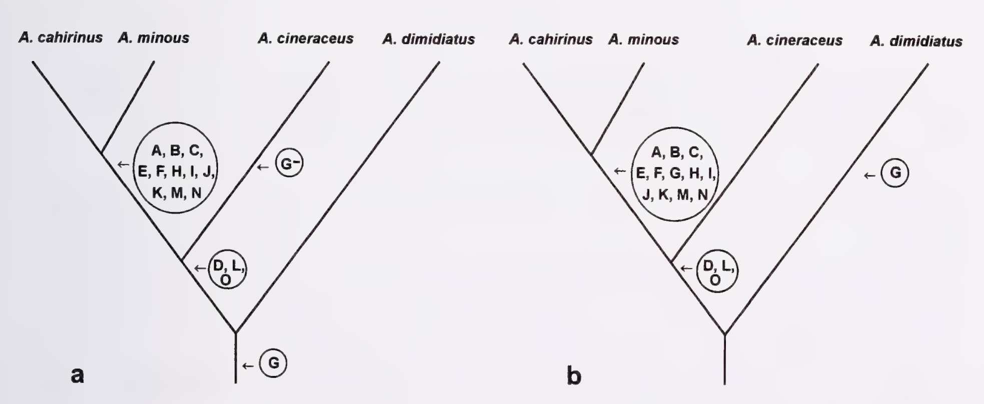


Fig. 7. Maximum parsimony tree, based on common Rbs. a) and b) differ with respect to the interpretation of G. Fusion events are indicated by resulting Rbs (A, B. . .O). Fission of Rb G is indicated by G^{-}.

appeared in Israel about 40 000 years ago (Tchernov 1968). The Cretan population was assumed to be founded by an ancestor with an all acrocentric karyotype (Denys et al. 1994).

From the chromosome tree of the four species we infer a different scenario of karyotype diversification. A common ancestor with a nearly all acrocentric karyotype – it probably contained Rb G – invaded Egypt about 120 000 and Israel about 40 000 years ago.

Waves of Robertsonian fusion started independently in Northern Africa and Israel. They led to a nearly all-metacentric state in the two species *A. cahirinus* and *A. dimidia-*

tus. Since the karyotypes from the Cretan species *A. minous* is very similar to that of the Egyptian species *A. cahirinus* we assume that Crete was populated by Egyptian *Acomys* after fixation of most Rb chromosomes. *Acomys* may have reached Crete by ship with humans. This assumption is in accordance with the lack of fossil *Acomys* records in Crete (Dieterlen 1978).

A corollary of this scenario is that Rb formation and fixation was a rapid process, at least in the Israelian spiny mice. The rate of Rb fixation (15 Rbs in 40 000 years) is, however, in accordance with estimates by Ferris et al. (1983). They estimated the rate of Rb fixation in *Mus musculus* to be 1 per 1 000 years.

Acknowledgements

The excellent technical assistance of C. Reuter is gratefully acknowledged.

Zusammenfassung

Karyotypische Verwandtschaftsbeziehungen zwischen vier Arten der Gattung Acomys (Rodentia)

In dieser Arbeit werden G-Banden Karyotypen von vier verschiedenen *Acomys* Arten aus verschiedenen Regionen beschrieben: *Acomys cahirinus* aus Ägypten, *A. cineraceus* aus dem Sudan, *A. dimidiatus* aus Israel und *A. minous* von Kreta. Die diploide Chromosomenzahl variiert erheblich zwischen diesen Arten und reicht von 2n = 36 bis 2n = 50. Die Unterschiede werden im Wesentlichen durch Robertson-Translokationen verursacht. Wir benutzen das Auftreten von gemeinsamen Robertson-Chromosomen in verschiedenen Arten als Merkmale zur Konstruktion eines Stammbaums.

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Z. Säugetierkunde **64** (1999) 230–238

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Mating behaviour of *Ctenomys mendocinus* (Rodentia, Ctenomyidae)

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Receipt of Ms. 04. 09. 1998
Acceptance of Ms. 01. 04. 1999

Abstract

This is the first description of mating behaviour in *Ctenomys mendocinus.* Observations were conducted in a transparent acrylic pipe, under dim red light. The description of the courtship and copulation stages was based on 18 trials (7 males, 9 females, 17 couples).

The mating behaviour of *Ctenomys mendocinus* was characterized by vocalizations, long courtship, long bouts of precopulatory interactions, lengthy intromissions, a brief copulation stage, aggressive copulatory postures, and mutual indifference after ejaculation. The mating and copulation patterns in *Ctenomys mendocinus* are similar to those of other solitary subterranean, phylogenetically unrelated, forms (e. g., *Spalax* and geomyids). This suggests that the copulatory behaviour of *C. mendocinus* is closely related to its social structure. On the other hand, the structure of precopulatory interactions in *C. mendocinus* is very much like that of some solitary and social bathyergids, possibly reflecting phylogenetic affinities.

Key words: *Ctenomys mendocinus*, copulatory behaviour, social biology

Introduction

The "tuco-tuco" *Ctenomys mendocinus* is a hystricomorph, fossorial, solitary rodent, and a seasonal breeder (Puig et al. 1992; Rosi et al. 1992), widely distributed throughout Argentina (Cabrera 1961; Honacki et al. 1982). In Mendoza province this species is found in different mountain environments and occurs in isolated groups of low density (Rosi et al. 1992). Our knowledge of the reproductive behaviour of the genus in general and of *Ctenomys mendocinus* in particular is limited. The only data on copulatory behaviour of the genus *Ctenomys* are those of Altuna et al. (1991), corresponding to *Ctenomys pearsoni* of Uruguay. As far as *C. mendocinus* is concerned, its mating and copulatory patterns are unknown. In her review on the patterns of behaviour of hystricomorph rodents, Kleiman (1974) regarded brief copulations as one of the typical behaviours in this sub-order. Hickman (1982) compared copulatory behaviour in *Cryptomys hottentotus* to that described for other subterranean rodents: *Spalax* (Nevo 1969) and geomyids (Andersen 1978; Schramm 1961). The differences (spontaneous nature of copulation and short intromissions in *Cryptomys hottentotus* vs. long courtship and long duration of intromissions in *Spalax* and geomyids) were explained by differences in social biology and burrow systems (social vs. solitary; copulations not restricted to particular areas vs. mating in specially constructed widened areas) (Hickman 1982). In contrast, Burda (1989) suggested that the basic characteristics of copulatory behaviour in *Cryptomys hottentotus* may relate to the common mating patterns exhibited by most hystricomorphs, and hence the differ-

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ences may also be phylogenetic. The hystricomorph condition of *Ctenomys mendocinus*, as well as its fossorial and solitary habits, led to the investigation whether its copulatory behaviour reflects its social system or its phylogenetic affinities. If this behaviour were linked with the social structure, *C. mendocinus* would differ from social subterranean hystricomorphs by exhibiting longer courtship, aggressive copulatory postures, lengthy intromissions, and aggressiveness or indifference toward the partner after mating. On the contrary, no differences would be apparent between *C. mendocinus*, and social hystricomorphs if its behaviour were mostly determined by the common, phylogenetically determined, mating pattern of hystricomorphs. DEWSBURY (1972) established four attributes for a comparative study of copulation in mammals: First, the male and female may or may not become firmly locked or tied together by a strong mechanical connection during copulation. Second, pelvic thrusting may or may not occur during insertion. Third, multiple insertions with no sperm transfer may or may not be prerequisite to the occurrence of ejaculation. Fourth, either a single ejaculation or multiple ejaculations might be attained (DEWSBURY 1972). As each of these four attributes has two alternatives, patterns of copulatory behaviour elaborated in this scheme can take any of 16 forms (DEWSBURY 1972).

Therefore, the main goals of this study were: a) to describe the mating behaviour of *C. mendocinus*, b) to assess whether its copulatory behaviour is consistent with HICKMAN's (1982) hypothesis, and c) to define the DEWSBURIAN (1972) copulatory pattern in *C. mendocinus.*

Material and methods

A total of 29 adults (16 females: 130–197 g; 13 males: 156–328 g) was live-trapped in Cacheuta (Province of Mendoza, Argentina, 1330 m a.s.l) during March for five successive years (1992–1996).

The animals were housed in a basement which received sunlight through a long narrow window above ground level. They were individually kept in plastic containers (50 cm wide × 40 cm high × 70 cm long) filled with alluvial soil to a depth of 3 cm. A 30-cm long, 9-cm diameter plastic pipe was provided for shelter. Temperatures ranged between 14 °C and 20 °C. Alfalfa, carrots, and lettuce were supplied ad libitum. No free water was provided. During June–August, males and females were periodically placed together in a transparent acrylic pipe (200 × 11 × 16 cm). Trials were conducted in dim red light between 10:00 and 14:00 h. The female was placed in the pipe 45 minutes before introducing the male. Trials started when the male was introduced into the pipe, and pairs were permitted approximately 1–1.5 h to initiate copulation. If copulation was initiated, observations were continued until attainment of the standard satiety criterion of 30 min with no intromissions (DEWSBURY 1975). All trials were video-taped. Trials observed totalled 174. Only trials with occurrence of copulations were considered in the analysis of mating behaviour. Therefore, the description of courtship and copulation was based only on the 18 trials in which copulation was attained (7 males, 9 females, 17 couples). Data are expressed as mean values (± SD) and/or ranges (mini.–max. values recorded).

Results

Mating patterns recorded in *Ctenomys mendocinus* are given in table 1. Both males and females were active from the start, seeking and slowly approaching each other, growling in a low-pitched voice. Some males and one female alternated growls with whines. Some males rubbed their perineal region against the pipe walls, and sometimes urinated (Fig. 1). On finding the urine of a female, males touched it with their nose for a few seconds. Upon encounters, partners sniffed at each other's genitalia, parted, and met again to engage in precopulatory interactions: with their mouths in right angles and their incisors locked together they swayed from side to side. On occasions this swaying movement made one of the animals fall on its back thus exposing abdomen and genitalia to the part-

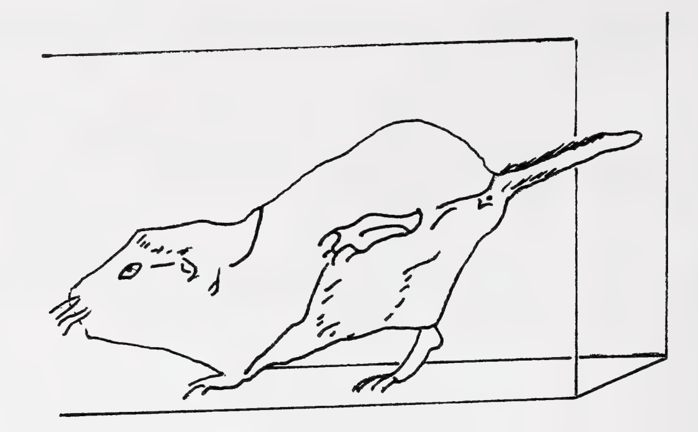


Fig. 1. Scent-marking behaviour of male of *C. mendocinus.*



Fig. 2. Mating foreplay of *C. mendocinus.*

ner (Fig. 2). The animals also stood on their hindfeet grasping each other's cheek with forefeet and teeth. This playful behaviour ended when one of the partners moved away. Some soliciting females mounted the males in much the same way as males mount females. A few females were initially inactive, reluctant to initiate courtship. They remained crouched, and exposed their incisors, ready to bite, when males came too close. Males responded to this threatening behaviour by presenting the side of the neck, half-closing the eyes and running away. In those cases where a male insisted on mounting a reluctant female, the female drove him back after a short fight. After fights like these, a few males emitted the guttural "tuc-tuc" sound typical of tuco-tucos before resuming courtship. The courtship stage was long (maximum duration: 3 900 sec, Tab. 1) and not continuous: partners played, parted, met again, and upon re-encounter courtship was resumed. First mounts occurred less than 8 min after the trial was started (Tab. 1), and were usually unsuccessful because of female resistance. In successful mounts the male mounted the female from behind, clasping her shoulders or lumbar region with his forefeet and biting her neck (Fig. 3). Occasionally the male held the female's hindfeet with his own. The female crawled away to escape, sometimes even carrying the male on her back. At first the male performed rapid shallow pelvic thrusts (PT), mostly without intromission, at a rate of 4 to 5 thrusts/sec. When the male achieved intromission, thrusts were deeper (DT) and slower (1 thrust/sec). Ejaculation, reached at the end of a number of deep thrusts, was obvious: the male grasped the female more strongly and a long lasting deeper thrust of 14 sec was discernible (SD = 10.01, range = 5–41), after which he dismounted slowly, and groomed his genitalia with forefeet and mouth.



Fig. 3. Copulatory posture of *C. mendocinus.*

Table 1. Mean duration ($\overline{X}$), standard deviation (SD), range, frequency (f) and number of observations (N) of mating and copulation patterns in *Ctenomys mendocinus.*

	$\overline{X}$ (sec)	SD (sec)	range (sec)	f	N
Mount latency	468	894	10–3 900		18
Intromission latency	616	905	14–3 900		18
Courtship	847	1056	60–3 900		18
Precopulatory interactions	44	74	2–437	4	74
Pelvic Thrusts (PT)	27	33	3–154	1	24
Deep Thrusts (DT)	53	31	5–130	1	24
Copulation	105	77	25–327	1	18
Copulation stage	256	200	40–777		18

Only two males whined during copulation, and one female uttered a high-pitched squeak as the male exercised his last thrust. Courtship was feebly resumed for a few minutes after copulation (Tab. 1), the animals walking up and down the pipe, growling and only occasionally locking their incisors until partners lost interest, and either crouched several centimeters apart or tried to escape by scratching the pipe walls until the end of the trial. A multiple-ejaculation pattern was absent in every trial. All episodes were ended by a single ejaculation. On nine of the trials ejaculation was achieved by the first mount with intromission. The remaining nine trials involved more than one mount but ejaculation was always attained on the last one. Mounting frequency was 2 (range 1–5), and the copulation stage lasted, at the most, 777 sec (Tab. 1).

Discussion

The mating behaviour of *C. mendocinus* was characterized by vocalizations, long courtship, long bouts of precopulatory interactions, a lengthy intromission, a brief copulation stage, aggressive copulatory postures, and mutual indifference after ejaculation. Tuco-tuco females did not show any typical soliciting behaviour (e. g. lordosis), yet they were active, frequently starting the precopulatory interactions and occasionally mounting the male.

As in other subterranean mammals, chemical (Nevo et al. 1976; Gorman and Stone 1989, 1990; Burda et al. 1990; Heth et al. 1992; Menzies et al. 1992) and chemosensory perception (Heth and Todrank 1995) can be very important in *Ctenomys mendocinus.*

Table 2. Mating and copulation patterns in hystricomorph and other subterranean rodents of different social structures.

Species	Courtship Length (sec)	Ejaculatory Intromission Length (sec)	Copulatory Posture	Post-mating behaviour of partners	Social structure	Sub-order	References
Geomys bursarius		15	aggressive		Solitary	Sciuromorpha	SCHRAMM (1961)
Thomomys talpoides		30–900	aggressive	male rebuffed	Solitary	Sciuromorpha	ANDERSEN (1978)
Spalax ehrenbergi	480–3 300		aggressive	male indifferent	Solitary	Myomorpha	NEVO (1969)
Georychus capensis				male chased	Solitary	Hystricomorpha	BENNETT and JARVIS (1988 a)
Cryptomys hottentotus	30	1–5	clumsy	soliciting female	Social	Hystricomorpha	HICKMAN (1982)
Cryptomys damarensis		30		male not chased	Social	Hystricomorpha	BENNETT and JARVIS (1988 b); BENNETT (1990)
Cryptomys mechowi		brief		female pulling away from the male	Social	Hystricomorpha	BENNETT and AGUILAR (1995)
Heterocephalus glaber		<15	clumsy	soliciting female	Highly Social	Hystricomorpha	JARVIS (1991)
Ctenomys mendocinus	60–3 900	25–327	aggressive	mutual indiffererence	Solitary	Hystricomorpha	This study

Tuco-tuco males become informed about the reproductive status of females by contacting the urine with their noses. The posture taken by males while rubbing their anogenital region allows them to mark the walls of their burrows, resembling the behaviour of *Spalacopus* i. e. urinating on vertical surfaces using a leg lift (KLEIMAN 1974). Vocal communication is involved in mating behaviour of solitary species, e. g. *Spalax* (NEVO et al. 1987; HETH et al. 1987). In *Ctenomys pearsoni* only females whine, which indicates their full receptivity to courtship (FRANCÉSCOLI 1995). Growls and whines in *Ctenomys mendocinus* are a signal of non-aggressiveness, and indicative of the animals' willingness to copulate. Their long bouts of precopulatory interactions help to coordinate the mating behaviour, disminishing the partners' fear and hesitation. Notwithstanding, precopulatory interactions might also play an important role in mating assessment, not just synchronisation of motivational states.

The courtship of the solitary hystricomorph rodent *Ctenomys mendocinus* was longer than that of the social hystricomorph *Cryptomys hottentotus* (HICKMAN 1982), whereas it was similar in length to the courtship of the solitary myomorph *Spalax ehrenbergi* (NEVO 1969). Likewise, the duration of ejaculatory intromissions of *C. mendocinus* was similar to that of the solitary sciuromorph *Thomomys talpoides* (ANDERSEN 1978) but longer than

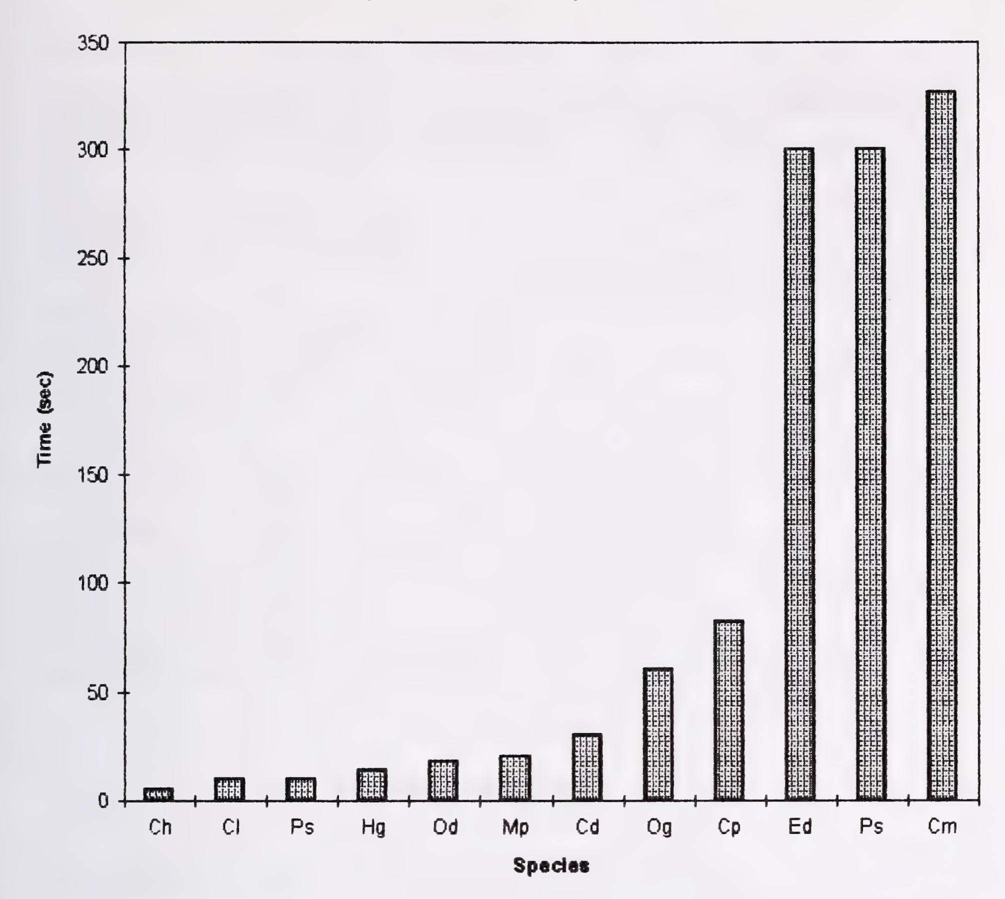


Fig. 4. Maximum duration of ejaculatory mounts in *Ctenomys mendocinus* and other hystricomorph rodents expressed in seconds. Abbreviations: Ch = *Cryptomys hottentotus* (HICKMAN 1982), Cl = *Chinchilla laniger* (BIGNAMI and BEACH 1968), Ps = Pediolagus salinicola (in KLEIMAN 1974), Hg = *Heterocephalus glaber* (JARVIS 1991), Od = *Octodon degus* (KLEIMAN 1974), Mp = *Myoprocta pratti* (KLEIMAN 1971), Cd = Cryptomys damarensis (BENNETT and JARVIS 1988 b), Og = *Octodontomys gliroides* (KLEIMAN 1974), Cp = *Ctenomys pearsoni* (ALTUNA et al. 1991), Ed = *Erethizon dorsatum* (SHADLE 1946), Ps = *Proechimys semi-spinosus* (MALINIAK and EISENBERG 1971), Cm = *Ctenomys mendocinus* (present study).

the duration in social hystricomorphs, such as *Cryptomys hottentotus* (HICKMAN 1982), *Cryptomys damarensis* (BENNETT and JARVIS 1988 b; BENNETT 1990), *Heterocephalus glaber* (JARVIS 1991), and also the solitary sciuromorph *Geomys bursarius* (SCHRAMM 1961) (Tab. 2). The long ejaculatory intromission of some solitary hystricomorphs like *Ctenomys mendocinus*, *Erethizon dorsatum* (SHADLE 1946), and *Proechimys semispinosus* (MALINIAK and EISENBERG 1971) (Fig. 4) would be exceptions to the basic pattern of hystricomorph rodents reported by KLEIMAN (1974), which involves brief copulations 5–10 sec long. On the other hand, mating and copulation patterns of *C. mendocinus* are consistent with HICKMAN's (1982) predictions according to which solitary subterranean rodents show long courtship, aggressiveness and lengthy intromissions during copulatory behaviour. This evidence suggests that the copulatory behaviour of *C. mendocinus* is more closely related to social structure (solitary life) than to phylogeny.

On the other hand, the structure of precopulatory interactions in *C. mendocinus* (e.g. locked incisors) is very much like the precopulatory interactions in *Georychus capensis* (Jarvis and Bennett 1991), the playful behaviour of *Cryptomys hottentotus* (Burda 1989), the incisor fencing between young of *Heterocephalus glaber* (Lacey et al. 1991) and sparring between young of *Cryptomys damarensis* (Bennett and Jarvis 1988b), possibly reflecting phylogenetic affinities.

As previously stated, Dewsbury (1972) established four attributes for a comparative study of copulation in mammals based in the presence or absence of lock, intravaginal thrusting, multiple intromissions, and multiple ejaculations.

C. mendocinus failed to exhibit lock, but it did show intravaginal thrusts. Although more than one mount with intromission was required in four of 18 tests, this appears to be attributable to the resistance offered by females in such occasions. As to whether an episode may either be terminated or not by a single ejaculation, it is likely that there will be more overlap between these two alternatives than for the first three criteria (Dewsbury 1972). Although *C. mendocinus* is likely to resume copulation after the first ejaculation, in none of the 18 tests did second ejaculations occur within 30 min of the first one. The capacity to attain ejaculation on the first vaginal penetration and the absence of multiple ejaculations suggest that *C. mendocinus* conforms to pattern twelve (absence of lock, presence of intravaginal thrusting, absence of a multiple-intromission pattern, absence of a multiple-ejaculation pattern) of Dewsbury's (1972) scheme unlike *Ctenomys pearsoni* (Altuna et al. 1991), *Spalax ehrenbergi* (Nevo 1969), *Cryptomys hottentotus* (Hickman 1982), and *Thomomys talpoides* (Andersen 1978) that conform to pattern nine (absence of lock, presence of intravaginal thrusting, presence of a multiple-intromission pattern, presence of a multiple-ejaculation pattern).

Acknowledgements

I would like to thank Ing. V. Roig who helped to make this work possible. The manuscript was improved by the critical comments of Dr. L. Marone and Dr. P. Black. I also thank Nelly Horak for translating the manuscript, Patricia Díaz for writing the German summary and Sonia Demaría for the illustrations. This work is in partial fulfillment of the requirements for a doctoral degree for S. Camín to be presented at the University of San Luis, Argentina.

Zusammenfassung

Paarungsverhalten von Ctenomys mendocinus (Rodentia: Ctenomyidae)

Dieses ist die erste Beschreibung des Paarungsverhaltens von *Ctenomys mendocinus*. Die Beobachtungen wurden in einem durchsichtigen Rohr aus Plastik durchgeführt. Die Beschreibungen von Brunst und Kopulation basieren auf 18 Tests (7 Männchen, 9 Weibchen, 17 Begattungen). Das Paarbildungsverhalten von *Ctenomys mendocinus* war durch Beschwichtigungslaute, lange Brunst, lange Spielsequenzen, eine lange Intromissionszeit, kurze Kopulation, aggressives Kopulationsverhalten und gegenseitige Gleichgültigkeit nach der Ejakulation gekennzeichnet. Das Paarbildungs- und Kopulationsmuster von *C. mendocinus* ähnelt dem solitär und subterran lebender Gattungen, die nicht näher verwandt sind, wie *Spalax* und Geomyiden. Dieses läßt vermuten, daß das Kopulationsverhalten von *C. mendocinus* eng mit der Sozialstruktur verbunden ist. Auf der anderen Seite, ist die Spielstruktur bei *C. mendocinus*, der einiger Gattungen der Familie Bathyergidae sehr ähnlich. Dieses spiegelt sehr wahrscheinlich hystricomorphe Verwandtschaft wider.

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INTERNATIONAL JOURNAL
OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Free-ranging Vampire bats (*Desmodus rotundus*, Phyllostomidae) survive 15 years in the wild

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Receipt of Ms. 12. 06. 1998
Acceptance of Ms. 12. 10. 1998

Key words: *Desmodus rotundus*, vampire, Chiroptera, Phyllostomidae, longevity

While there is considerable information on the life-span of bats of temperate zones, few data have been published about the life-span of tropical bats (see review by Tuttle and Stevenson 1982). The Phyllostomidae or American leaf nosed bats of the Neotropics are in general much less extensively studied, their habitats are less accessible and they do not have periodic seasonal inactivity, which facilitates collection of survival data for temperate zone bats (Davis and Hitchcock 1995). Reports exist only for some well-studied locations and a few abundant species. For example, *Artibeus jamaicensis* have been studied extensively on Barro Colorado Island in Panama. One animal was reported reaching 7 years (Wilson and Tyson 1970) while two others were at least nine years old (Gardner et al. 1991).

Vampire bats (*Desmodus rotundus*: Phyllostomidae) have been studied longer than most the other neotropical bat species because of their potential economic impact. During his studies on social behavior in *Desmodus rotundus* one of the authors (GSW) banded over 600 vampire bats at various places in Costa Rica, primarily in Guanacaste province, but also in Atlantic rainforest at the La Selva Biological Station.

On November 21st, 1994 MT caught a female *Desmodus rotundus* carrying band no. 507 at the Sendero Cave at Santa Rosa National Park (Guanacaste Province). The animal was pregnant and appeared to be in good condition. This bat was initially banded May 16th, 1980 at precisely the same location by GSW. During a visit to this cave in July 1994, GSW failed to observe any of the more than 300 vampire bats banded there between 1980 and 1982. Subsequent frequent netting in the area between June of 1996 and June of 1997 revealed no more banded vampire bats (M. T. Fernandez, Universidad Nacional de Costa Rica, pers. comm).

A second noteworthy record occurred at La Selva Biological Station (Heredia Province) on January 6th, 1996 when we recaptured another female vampire bat with an orange-green plastic band. This bat had been marked initially by GSW on September 2nd, 1981. Judging from the condition of the nipples this animal was lactating or postlactating. The distance between place of banding and recapture is approximately 2 km. While the animal was first caught at a roost in a big hollow *Dipteryx panamensis* located in primary forest near abandoned plantations, the recapture location is located at the edge of the La Selva property and serves probably as a flyway for animals roosting in old trees to the cattle pastures outside La Selva, as indicated by frequent captures of the species at that

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spot. GSW banded 50 vampire bats in 1981 at La Selva, and the reported animal is the first recapture known to us at the rather well-netted field station.

It is noteworthy that both of our recaptures were females. Wilkinson (1985) reported that female vampire bats form roost associations which remain stable over long periods. At the time of first capture, neither female was pregnant or lactating but both had average adult forearm lengths and weights, indicating that they were probably near one year of age when captured. Our observations indicate, therefore, that *Desmodus rotundus* females can remain reproductively active until at least 15 years of age. While there is indirect dental evidence for 18 year old vampire bats (Lord et al. 1976), the animals reported here represent, together with similar aged animals (1♂/2♀) reported by Delpietro et al. (1992), at an age of 15 years, the oldest recaptured vampire bats from the wild. Female vampire bats appear, therefore, to be able to live longer than the fruit bat *Artibeus jamaicensis*, which is about the same body size and occurs in similar locations in the New World tropics. While we cannot determine if this difference in life history is due to a difference in diet or behavior, we suspect that the tendency of female vampire bats to share food under duress (Wilkinson 1984) represents an important behavioral adaptation that can increase longevity. In general terms our observations emphasize the remarkable status of bats as small mammals with small offspring-numbers per birth and a comparably long life-span.

Acknowledgements

MT's work in Costa Rica was supported by a grant from the German Academic Exchange Service (DAAD), HSPII/AUFE and the DFG. For support in the field we want to thank K. Stoner (Universidad de Costa Rica) as well as C. Voigt and M. Holderied (University of Erlangen, Germany). Maria Teresa Fernandez (Programa Regional en Manejo de Vida Silvestre, UNA, Costa Rica) shared her unpublished data on Santa Rosa bats with us.

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Z. Säugetierkunde **64** (1999) 241–245

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

The use of day roosts and foraging grounds by Natterer's bats (*Myotis nattereri* Kuhl, 1818) from a colony in southern Germany

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Receipt of Ms. 23. 11. 1998
Acceptance of Ms. 15. 04. 1999

Key words: *Myotis nattereri*, telemetry, foraging, roosting, activity

Natterer's bat (*Myotis nattereri* Kuhl, 1818) occurs from SW-Europe and N-Africa through W-Asia (Horacek and Hanak 1983). Little is known about its ecology, though fecal analysis indicates that prey is caught close to or from vegetation (Gregor and Bauerova 1987; Shiel et al. 1991; Beck 1991, 1995; Taake 1992; Swift 1997). In behavioral experiments Natterer's bat is capable of detecting arthropods close to vegetation by echolocation, using signals of broad band-width (Siemers and Schnitzler unpubl. data).

In the course of a field study on echolocation and foraging behavior, we fitted three *M. nattereri* with radiotransmitters in order to locate their hunting areas. Here we present data on activity pattern, home range, and hunting area. Additionally, data on use and types of day roosts are given.

The study was conducted in the vicinity of Mössingen, Baden-Württemberg, Germany on the foothills of the Swabian Alb (48°23′N, 9°01′E) from May through August 1996 (radiotracking between July 24th and August 15th). The study area is situated between 470 and 700 m above sea level and is characterized by fruit tree orchards, beech-dominated deciduous forests, and monocultures of spruce (*Picea abies*). Villages and roads lie interspersed.

A colony of *M. nattereri*, comprising 50–60 animals distributed over several day roosts, was studied. Three adult non-lactating females (animal A1 through A3) were fitted with crystal-pulsed transmitters (BD-2A and BD-2B supplied by Holohil Systems Ltd., Ontario, Canada) weighing 0.6–0.7 g (6–7 % of the animals' body weight). The bats were tracked using FT 290-receivers (Andreas Wagner Telemetrieanlagen, Cologne, Germany) connected with 5-element Yagi antennae. Whenever we had radio contact, bearings were taken at 5 min intervals. With two observers at hand, two bearings were taken at the same time from different locations and an animal's position was determined by triangulation using the computer-program Tracker (Camponotus AB, Solna, Sweden). Home ranges and core hunting areas were determined from fixes obtained by triangulation. The home range was defined as the smallest convex polygon comprising all fixes of an animal. The core convex polygon comprising 50 % of the fixes was considered as the core hunting area. Additionally, with only one observer at hand, we monitored the temporal use of the core hunting areas. We obtained telemetric data for animal A1 from 8 nights, for A2 from 6 nights, and for A3 from 3 nights. Radio contact was maintained for about 70 % of the time spent monitoring A1 and for approximately 80 % and 55 % for A2 and A3, respectively.

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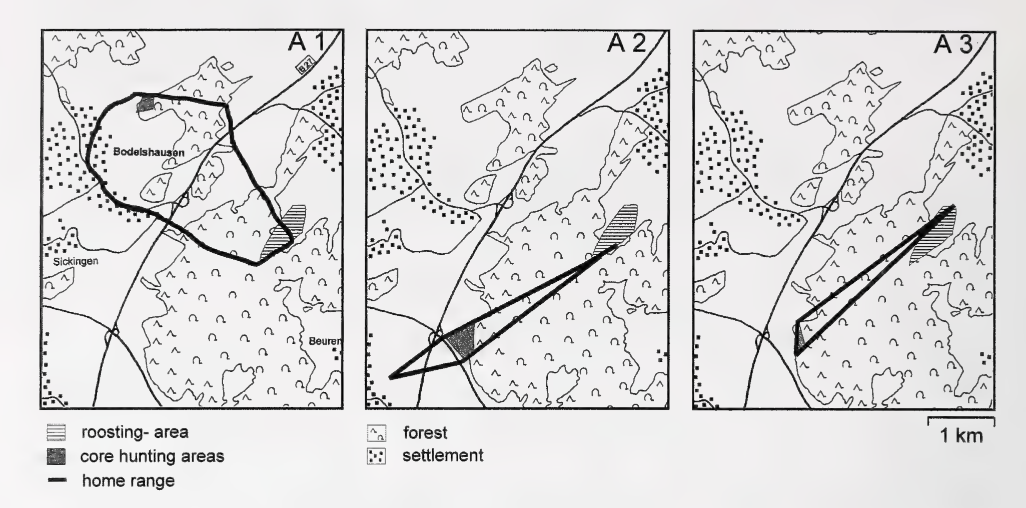


Fig. 1. Home ranges (minimum convex polygon containing all radio fixes) and core hunting areas (core convex polygon containing 50 % of fixes) of three adult female *Myotis nattereri* (A1, A2, A3). The roosting area encompasses 13 artificial and natural roosts used by the colony under study.

The colony under study roosted in bird nest boxes and artificial bat roosts, hung in the freestanding trees of an orchard belt. Between 3 and 30 individuals occupied a single roost at a time. By radio-telemetry we found a day roost in a hollow branch of a beech-tree (*Fagus sylvatica*) at 7 m height on the slope of a forested hill. During a hot period, animal A1 roosted therein for two consecutive days, on the second of which seven Natterer's bats were counted leaving the roost. We discovered a total of 13 day roosts within a minimum convex polygon of 24.3 ha; about 90 % of it being orchards and 10 % hilly mixed forest (Fig. 1). As established by inspection of roost sites, the colony changed roosts at least 12 times in 11 weeks (May 1st to July 23rd). On one occasion, we discovered about 20 Natterer's bats in an artificial bat roost together with a hornet queen (*Vespa crabo*) on its newly built nest.

The first bats emerged from a roost 31.6 ± 9.6 min (mean ± standard deviation, n = 24) after local sunset and the last ones returned to the roost 39.6 ± 9.9 min (n = 19) before local sunrise, as monitored visually. Time between sunset and emergence and return and sunrise, respectively, remained fairly constant from May through August; thus the animals' active period was more than 1.5 h shorter in mid-summer than in spring and fall (Fig. 2).

The home ranges, determined from radio fixes, measured 523 ha in A1, 123 ha in A2, and 80 ha in A3 (Fig. 1). The home range of A2 would have extended to approx. 580 ha if we had included one night (7./8. August) during which we followed A2 without being able to triangulate. Core hunting areas within those home ranges covered 2.8 ha for A1 and 18.6 ha for A2. Due to a lack of sufficient fixes for A3, we could not determine the size but only the rough position of the bat's core hunting area (Fig. 1). The bats' presence in their core hunting area could be confirmed on each of 9 nights of inspection with only one observer at hand. Out of a total of 24 h 15 min of tracking-time between 22:45 pm and 4:48 am across those 9 nights, individuals were present on average 56.6 % of the time in their core hunting area (A1: 86.2 %, A2: 46.8%, A3: 51.2%).

Centers of the core hunting areas were located at a distance of 3.1 ± 0.3 km (n = 3) from the roosting area. The animals were found up to a distance of 3.7 ± 0.7 km (n = 3) from the roosting area. With the exception of the immediate surroundings of the roosting area, the home range of A1 did not overlap with those of A2 and A3, whereas all fixes

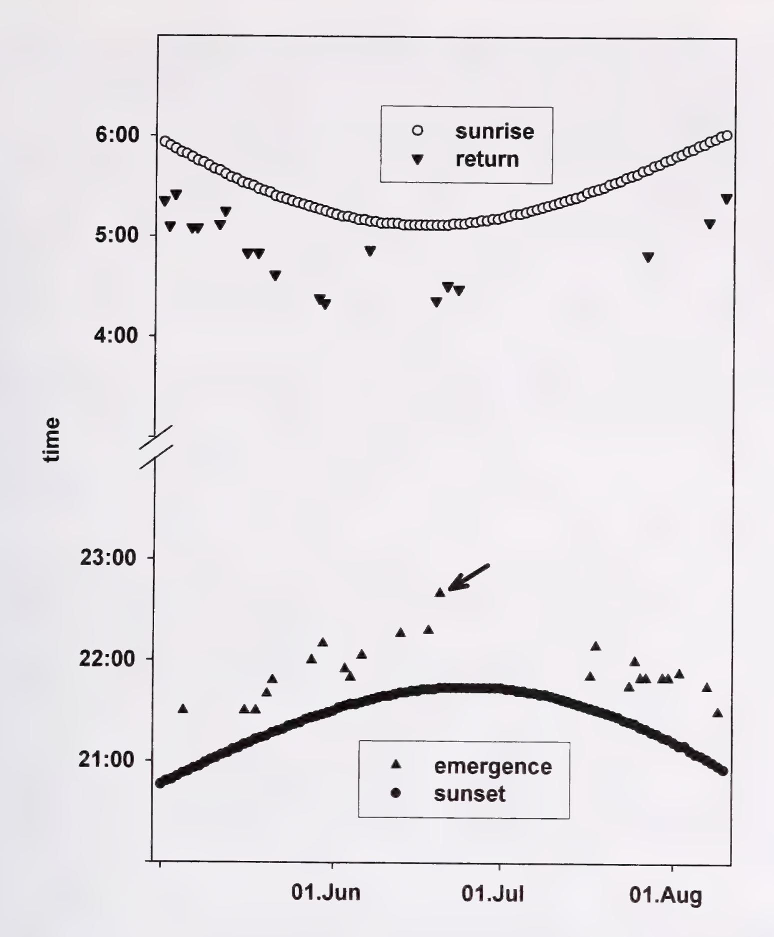


Fig. 2. Emergence of first (n = 24) and return of last (n = 19) *Myotis nattereri* in comparison with local sunset and sunrise between May 1st and September 10th 1996. On June 20th, the animals delayed emergence about 25 min, waiting for a bout of heavy rain to pass (arrow). Note break in time axis.

obtained for A3 lay within the home range of A2 (Fig. 1). In 3 nights we recorded the simultaneous presence of A1 and A2 in the same area. The core hunting areas of A1 and A2 were 3.9 km apart; those of A2 and A3 were adjacent.

The core hunting area of A1 comprised mixed deciduous forest, a monoculture of coniferous forest (*P. abies*), an area that had been deforested by a storm and recently replanted with oak (*Quercus* spp.) and margins of pasture; hence, an area rich in edge structures. The hunting areas of A2 and A3 were situated at the edge of a coniferous forest (*P. abies*) and included a fresh clearing and orchards with trees planted at distances between 10 and 30 m apart.

We conclude that animals were continuously on the wing, as signal direction kept changing most of the time. On one occasion only, it remained constant for 75 min while it was raining heavily, and the animal presumably hung in a sheltered place within a coniferous forest.

We first detected the animals in the core hunting area 84.3 ± 25.8 min (n = 9) after they had left the roost in the evening. When the bats were heading back from the hunting areas to the roosts in the morning they covered the distance with 5.7 ± 0.2 km/h

(mean ± sd, n = 3). From photographs under stroboscopic illumination, the flight speed of *M. nattereri* was determined to be 15.5 ± 3.2 km/h (n =10). Thus the animals could have reached their roosting areas nearly three times faster than they actually did. We conclude that the animals were hunting on their way to and from the core hunting area.

Our findings confirm that the activity period of *M. nattereri* depends on sunset and sunrise, and thus on light intensity, as well as on weather conditions (see Engländer and Laufens 1968; Laufens 1973; Swift 1997).

We found that Natterer's bats used individual core hunting areas at least during the study period; i. e. they showed site-fidelity. The existence of core hunting areas visited night after night is also reported for other European bat species, e. g. *Myotis myotis* (Audet 1990), *Myotis emarginatus* (Krull et al. 1991), and *Myotis daubentonii* (Arnold pers. comm.). By fidelity to individual, exclusive hunting grounds the bats could avoid intraspecific competition for resources (e. g. von Helversen 1989). From our data we cannot answer the question as to what degree core hunting areas overlap, but the simultaneous presence of A2 and A3 in the same area might indicate that some overlap occurs. Another advantage of small and hence well known core hunting areas could be that the bats establish a detailed cognitive map, improving orientation in space and the repeated use of rewarding feeding sites.

Concerning the habitat type used by *M. nattereri*, it is striking that coniferous forest was present in all of the three determined core hunting areas, whereas the study area is dominated by mixed deciduous forest. Extensive orchards were present in two of the core hunting areas. All core hunting areas were rich in horizontal and vertical edges. The hypothesis that *M. nattereri* hunts close to edges of vegetation is supported indirectly by fecal analysis (Gregor and Bauerova 1987; Shiel et al. 1991; Beck 1991, 1995; Taake 1992; Swift 1997), predictions from wing morphometry (Norberg 1981) as well as behavioral experiments on detection ability (Siemers and Schnitzler unpubl. data) and directly by visual observation in the field (Arlettaz 1996; Swift 1997; Siemers and Schnitzler unpubl. data). The data presented here do not conflict with this view of *M. nattereri's* foraging ecology, but the spatial resolution of telemetry is too coarse for explicit confirmation.

In our study we found a distance between roosting area and core hunting areas of about 3 km for *M. nattereri. Myotis blythii, M. daubentonii*, and *M. myotis* travel about 4 km, 6–8 km, about 9 km and even up to 25 km between roosting and core hunting areas, respectively (Audet 1990; Arlettaz 1995; Arnold pers. comm.). From these considerable distances it may be concluded that intraspecific competiton forces individuals to hunt at some distance from roosts (von Helversen 1989), or that core hunting and roosting areas are chosen according to different criteria. Hunting grounds should yield abundant and accessible prey, while roosting areas should provide roosts protecting the bats from predators, providing a favorable micro-climate (Lewis 1995) and enough space for conspecifics, especially in nursing colonies. The roosting area of the colony under study is characterized by a high density of bird nest boxes and artificial bat roosts, most of which are well exposed to the sun in spring, when the crowns of the free-standing fruit trees are still leafless. We presume that the abundance of possible roosts and their warm temperature compared to hollow trees in the middle of a forest make the roosting area favorable. The localization of one day roost within a forest neighboring the orchard during a hot period had led us to speculate whether the bats might choose roosts in the cooler forest during hot summer days. The Natterer's bats changed roosts often and are, according to Lewis (1995), to be categorized as low roost-fidelity species. As the bats changed frequently from one roost to another in the immediate vicinity, climatic differences are unlikely to play a major role and we consider the avoidance of parasites to be an important factor for those changes (e. g., Laufens 1973; Lewis 1995).

Acknowledgements

We thank Elisabeth Kalko, Esther Langeheinecke, Gisela Lotter, and Wibke Thies for discussion and valuable suggestions, the forestry authority of Mössingen for logistic support, Andreas Beig, Dietmar Nill, Kai Siemers, and Albrecht Rilk for help in the field and Niamh Ni Bhleithin and Robert Paxton for correcting the English.

Licenses: Naturschutzrechtliche Ausnahmegenehmigung 73-8/8852.21 / RP Tübingen; Versuchsfunkgenehmigung 77 55 9985 / BAPT Schwäbisch Hall

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Z. Säugetierkunde 64 (1999) 246–250

http://www.urbanfischer.de/journals/saeugetier

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Genetic relatedness in two Southern sea lion (*Otaria flavescens*) rookeries in the southwestern Atlantic

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Receipt of Ms. 23. 06. 1998
Acceptance of Ms. 25. 03. 1999

Key words: *Otaria flavescens*, protein electrophoresis, genetic distance

The southern sea lion, *Otaria flavescens* (Shaw, 1800), is distributed along the coast of South America, from Torres (29°20′ S 49°43′ W) in southern Brazil in the Atlantic Ocean (Rosas et al. 1994) to Cape Horn in the extreme south, and from Cape Horn to Zorritos (4° S) in northern Perú in the Pacific Ocean (Riedman 1990). The northernmost breeding grounds are along the coasts of Uruguay (Isla de Lobos, Cabo Polonio, and La Coronilla). A total of 15,000 individuals was estimated for this area. To the north of the Uruguayan breeding grounds, in southern Brazil, there are only two non-breeding rookeries where subadult males predominate. Seasonal movements have been documented for Rio Grande do Sul coast (Rosas et al. 1994). In addition, erratic records for the species have been reported from Rio de Janeiro (23° S) and even to 13° S (Castello 1984) but always by solitary individuals.

In Argentina, they breed along the Patagonian coast, from Punta Bermeja at 41°08′ S to 55° S on Tierra del Fuego Island. Presently, there are 54 breeding and non-breeding rookeries with a total of 51,000 individuals up to 47°05′ S, 66°16′ W (Reyes et al. 1999). Individual movements showing seasonal patterns have been demonstrated (Crespo 1988; Crespo and Pedraza 1991). To the north of the Patagonian grounds, there are only two subadult male rookeries in Buenos Aires Province at the Mar del Plata (38° S) and Quequén harbours 38°30′ S), as well as a breeding rookery at Isla Trinidad (39° S).

Biochemical-genetic data have been used as a powerful tool for studying population biology; moreover, they can provide much information about the population structure of a species. Taking into account the reduced information available with respect to migrations and interchange of individuals, the aim of this study was to analyse the genetic variability in the southern sea lion in two rookeries: Isla de Lobos, Uruguay and Punta Norte, Península Valdés.

Collection of samples: Blood samples were collected from 70 southern sea lion pups (less than 30 days old), during the 1992/93 breeding season, from two rookeries 1,300 km distant from each other: Isla de Lobos, Maldonado, Uruguay (35 blood samples) (35°02′ S, 52°55′ W) and Punta Norte, Península Valdés, Chubut, Argentina (35 blood samples) (42°04′ S, 63°47′ W) (Fig. 1). All pups sampled were selected at random from breeding harems at both localities. About 2 to 5 ml of heparinized peripheral blood was collected

0044-3468/99/64/04-246 $ 12.00/0



Fig. 1. Location of the study areas and of the geographical names mentioned in the text. ● Reference rookeries, ▲ Sites of sample collection.

from the extradural vein from the lumbar region. After blood extraction, pups were returned to their mothers.

Genetic analysis: Blood samples were processed in situ, in the field. Plasma and erythrocytes stored in liquid nitrogen were subjected to horizontal 5 %–7 % polyacrylamide gel electrophoresis (PAGE). Only 64 samples from the 70 collected were included for the electrophoretic interpretation. Nine protein systems representing 10 putative loci were analysed: lactate dehydrogenase A and B (LDHA, LDHB), malate dehydrogenase (MDH), phosphogluconate dehydrogenase (PGD), isocitrate dehydrogenase (IDH), superoxide dismutase (SOD), glutamate oxalacetate transaminase (GOT), and esterase D (ESD) from erythrocytes, and transferrin (TF) and albumin (ALB) from plasma. The proteins studied, the electrophoretic methods and staining procedures are given in table 1. To locate TF patterns, electrophoresis gels were run with human standards (HSA) and the genotypes were interpreted by direct comparison with them.

Genotypic frequencies were tested by maximum likelihood for Hardy-Weinberg equilibrium. Differences in gene frequencies between the two rookeries were tested by means of a two-tailed binomial test (Zar 1996). Observed and expected mean gene diversity values at population level (H_o and H_e) and Nei (1978) genetic distance (D) were calculated by using the Genetic Data Analysis (GDA) computer program (Lewis and Zaykin 1997).

From the 10 examined loci, nine were monomorphic and six of them as shown in Gales et al. (1989): GOT, LDHA, LDHB, MDH, PGD, SOD. Only TF was polymorphic for both sea lion rookeries, and curiously, it was monomorphic in southern elephant seals (Gales et al. 1989).

Table 1. Screened proteins in *Otaria flavescens*. Optimal buffer systems: 1) Tris-maleic-EDTA-magnesium chloride, pH 7,4 (SHAW and PRASAD 1970); 2) Tris-EDTA-citric acid, pH 7.0 (SHAW and PRASAD 1970); 3) Phosphate-EDTA-citrate, pH 6.9 (SCHNEIDER 1988); 4) Phosphate-citric acid, pH 5.9 (HARRIS and HOPKINSON 1976); 5) Lithium hydroxide-boric acid, pH 8.3 (BOUMAN and BEARN 1965). Staining methods references: a) HARRIS and HOPKINSON (1976); b) HILLIS and MORITZ (1990); c) SCHNEIDER (1988).

System	Abbreviature and enzyme commission number	Optimal buffer system	Staining method reference
1. Erythrocyte enzymes			
Lactate dehydrogenase	LDH 1.1.1.27	1	a
Malate dehydrogenase	MDH 1.1.1.37	2	a
Phosphogluconate dehydrogenase	PGD 1.1.1.44	3	a
Isocitrate dehydrogenase	IDH 1.1.1.42	4	a
Superoxide dismutase	SOD 1.15.1.1	4	a
Glutamate oxalacetate transaminase	GOT 2.6.1.1	2	b
Esterase D	ESD 3.1.1.1	3	a
2. Serum proteins			
Transferrin	TF	5	c
Albumin	ALB	5	c

The same alleles of TF were found at PN and IL. Two alleles and three different electrophoretic TF phenotypes were observed. Both TF 1 and TF 2 bands showed slower electrophoretic mobility than that of human TF C. The heterozygotes TF 1–2 showed a two-banded pattern, consistent with the monomeric molecular structure of this protein.

Under the assumption that genotypes are determined by two different alleles, the genotype distribution in both populations was in Hardy-Weinberg equilibrium according to the maximum likelihood estimation (Tab. 2). The allele Tf^2 was the most frequent in both sample sites. The two tailed binomial test showed that the gene frequencies were significantly different for the stocks ($\varepsilon = 2.5897$, $p < 0.01$). The sample size could explain in part the observed differences in the gene frequencies. TF is usually a good molecular marker that is polymorphic in many mammals (GOODMAN et al. 1965; SHAUGHNESSY 1969; HERZOG et al. 1991; HARTL and FERRAND 1993), and as it showed polymorphism in the present study it could be used as a molecular marker according to the different frequencies found.

Observed genetic heterozygosity for southern sea lions at Isla de Lobos was $H_o = 0.027$ and $H_o = 0.003$ for Punta Norte. These H values are in the extremes of previous values given for other pinniped species (GALES et al. 1989). It has been stated that

Table 2. Observed transferrin phenotypes, allele frequencies, expected and observed mean heterozygosity (He and Ho) and an estimate of the fixation index (f) in the two studied rookeries of *Otaria flavescens.*

Rookery	Number of individuals of each phenotype			Gene frequencies		He	Ho	f
	1-1	1-2	2-2	Tf^1	Tf^2			
PUNTA NORTE	0	1	33	0.0147	0.9853	0.002941	0.002941	0.00000
ISLA DE LOBOS	2	9	19	0.2167	0.7833	0.032542	0.026667	0.18309

marine mammals as a group are low in genetic variation (Saughnessy 1975; McDermid and Bonner 1975; Lidicker et al. 1981; Gales et al. 1989); however the H value for PN is extremely low, probably as a consequence of a bottleneck effect. Between the 30's and the 50's, the southern sea lion population in northern Patagonia was reduced to about 10 % of its original size remaining in a stable condition between 1975 and 1991. They were heavily exploited, mainly from Península Valdés and Tierra del Fuego, by national permissioners for leather and oil. In Península Valdés, the population was reduced during this period from 200,000 to less than 15,000 individuals (Crespo and Pedraza 1991). Presently, there are 35,000 individuals and the population is increasing at a rate of 3.5 % per year (Crespo pers. comm.).

On the other hand, the H value of IL is one of the highest found in pinnipeds according to Gales et al. (1989). One reason may be that another pinniped species, the southern fur seal *Arctocephalus australis*, has been the main exploited species in Uruguay instead of *O. flavescens*. However, Vaz-Ferreira (1979) stated 30,000 individuals of *O. flavescens* for 1954, and between 1986 and 1990 Lima and Batallés (pers. comm.) estimated 15,000 individuals, reaching the lowest number ever known for this stock and with a decreasing trend.

The Nei genetic distance obtained between Punta Norte and Isla de Lobos was D = 0.003. This is a low value compared with intraspecific values found from populations of other mammalian species (Selander and Johnson 1973). There are no previous reports of genetic distances for conspecific pinnipeds except for *M. leonina* from Macquarie and Heard Islands (D = 0.007, Gales et al. 1989).

Taking into account that individual movements between Patagonian and Uruguayan stocks have been recorded from marked animals (Lorenzani and Lorenzani, pers. comm.), this suggests a high mobility of individuals between rookeries, especially considering the low number of marked animals from sites with several hundreds or thousands individuals. In this opportunity, the presence of the same fixed allele at each of the nine monomorphic loci and the low value of genetic distance leads to the conclusion that both rookeries belong to the same population in which gene flow is currently occurring.

Acknowledgements

The authors are indebted to many people who helped in the field sampling. We thank Centro Nacional Patagónico (CONICET, ARGENTINA) and Instituto Nacional de Pesca (Uruguay) for their logistical support in the field, P. Schwarzbaum and R. Werner for their critical review of the manuscript and the anonymous referees for their comments and suggestions. We also thank financial support through the Binational Project (1992–93) for Uruguay and Argentina E. C. and H. L. C. grant from Marine Mammal Action Plan (UNEP) and UBACYT EX 228/95–97 and CONICET 211/97–99 M.M grants.

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Z. Säugetierkunde **64** (1999) 251–255
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Seasonal occurrence of killer whales (*Orcinus orca*) in waters of Rio de Janeiro, Brazil

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Receipt of Ms. 16. 02. 1999
Acceptance of Ms. 21. 04. 1999

Key words: *Orcinus orca*, occurrence, Rio de Janeiro coast, Brazil

Killer whales (*Orcinus orca*) are found in all oceans and seas, from the polar regions to the equator, in both hemispheres. However, they appear to be more common near shores in cold temperate to subpolar waters (Jefferson et al. 1993). Records of killer whales are few or nearly absent for most parts of the Brazilian coast. The first reported Brazilian record is a stranding 128 km north of Rio Grande (31°57′ S), southern Brazil (Castello 1977). Additional records have remained anecdotal (e. g. Castello and Pinedo 1986; Daniel et al. 1992; Santos and Siciliano 1994) and only one stranding record is known for the Rio de Janeiro coast (Geise and Borobia 1988). More recently, a study on killer whale interactions with the swordfish and tuna fishery was conducted south and southeastern of Brazil (Dalla Rosa 1995). A collection of recent sightings of killer whales for the Rio de Janeiro State coast (21°37′ S–23°10′ S) is presented and provides an opportunity for discussion of their presence and ecological requirements in an area previously uncovered.

Information on killer whale presence was provided through the implementation and development of a sighting network along the Rio de Janeiro coast. The data set was analysed to study individual occurrence and location patterns, based on characteristics that can be used to identify individuals uniquely (i. e. dorsal fin, saddle patch; Bigg et al. 1987; O'Sullivan and Mullin 1997).

A total of 29 records of killer whale groups was confirmed on the coast of Rio de Janeiro for the period between October 1993 and November 1997 (Tab. 1, Fig. 1). One additional record was obtained for November 1983. The period between August 1996 and February 1997 represents 76.7 % of all sightings. Killer whale sightings were concentrated on spring and summer months, accounting for 93 % of all confirmed records. Group size ranged from one to 15 individuals, but averaged 3.9 animals. Four groups included at least one adult male, and four groups at least one calf. Four individual killer whales have been photoidentified to date on the coast of Rio de Janeiro. While not every individual was photographed from each group, catalogued photographs showed that at least one individual was resighted at a time interval of 37 days. All groups sighted were found in shallow coastal waters, well located inside the continental slope. The furthest offshore sighting was 38.9 n. miles off Atafona (21°35′ S), the northern coast of the state. The fact that most records are known for the area between Búzios (22°44′ S) and the city of Rio de Janeiro (22°56′S) may suggest higher chances for opportunistic sightings due to the increased human recreational activity during the warmer months. However, this observed seasonality

0044-3468/99/64/04–251 $ 12.00/0

Table 1. Sighting records of killer whales (*Orcinus orca*) on the coast of Rio de Janeiro, Brazil.

Map key	Date	Location	Depth (m)	Group size	Remarks	Source
1	November 1983	Praia de São Conrado, Rio de Janeiro	<20	2+	located close to the surf zone	This study
2	16 October 1993	Palmas Inlet, Ilha Grande bay	10–15	4	adult male, mother-calf and a juvenile; fast swimming	P. Bianco
3	March 1994	Pau a Pino and Meio Is., Ilha Grande bay	10–15	3	adult male, adult female and a juvenile	This study
4	21 October 1994	Praia da Armação, Búzios	10–12	4	adult male, adult female and juveniles	E. Fernandes
5	21 October 1994	Praia da Armação, Búzios	<20	5	reported	E. Fernandes
6	12 July 1995	off Atafona	<30	4	04:30 PM	A. P. Di Benedito and R. Ramos, pers. com.
7	20 August 1996	38,9 n off Atafona	30	3	02:30 PM	A. P. Di Benedito and R. Ramos, pers. com.
8	September 1996	29 n off Atafona	20	1	02:30 PM	A. P. Di Benedito and R. Ramos, pers. com.
9	02 October 1996	6,4 n off Iquipari	14	1	11:20 PM	A. P. Di Benedito and R. Ramos, pers. com.
10	23 November 1996	Praia do Foguete, Cabo Frio	<20	ca. 15	at least one adult male and several juveniles; located close to the surf zone	This study
11	30 November 1996	Búzios	<20	3	located close to the surf zone	This study
12	01 December 1996	Geribá, Búzios	<20	3	possibly the same group sighted the day before, located close to the surf zone	This study
13	15 December 1996	Jaconé, Saquarema	<20	3	located close to the surf zone	This study
14	18 December 1996	Praia do Foguete, Cabo Frio	<20	ca. 12	large concentration of rays in the sighting area; located close to the surf zone	This study

15	18 December 1996	Praia da Vila, Saquarema	<20	3	located close to the surf zone	This study
16	21 December 1996	Praia Seca, Araruama	<15	4	mother-calf and two juveniles, low speed swimming	This study
17	24 December 1996	Pesqueiro dos Cafés e dos Gatos, off Saquarema	<20	4	killer whales aprroached the fishing boat	This study
18	29 December 1996	Praia Seca, Araruama	<20	3	03:00 PM; located close to the surf zone	This study
19	30 December 1996	Praia Seca, Araruama	<20	3	slow speed swimming	This study
20	01 January 1997	Praia da Vila, Saquarema	<20	3	located close to the surf zone	This study
21	08 January 1997	Praia de Ipanema, Rio de Janeiro	<15	3	located close to the surf zone	This study
22	12 January 1997	Praia da Vila, Saquarema	<20	4	located close to the surf zone	This study
23	14 January 1997	Praia da Vila, Saquarema	<20	4	lob tailing, located close to the surf zone	This study
24	20 January 1997	Praia Seca, Araruama	<25	3	located close to the surf zone	This study
25	27 January 1997	Praia da Vila, Saquarema	<20	3	located close to the surf zone	This study
26	February 1997	Itaipuaçu, Niterói	<20	4	reported	This study
27	14 February 1997	Praia da Barra da Tijuca, Rio de Janeiro	<15	3	one killer whale attacking a ray; breaching	This study
28	16 February 1997	Praia Brava, Arraial do Cabo	<20	3	reported	This study
29	summer 1997	Búzios	<20	3	reported	This study

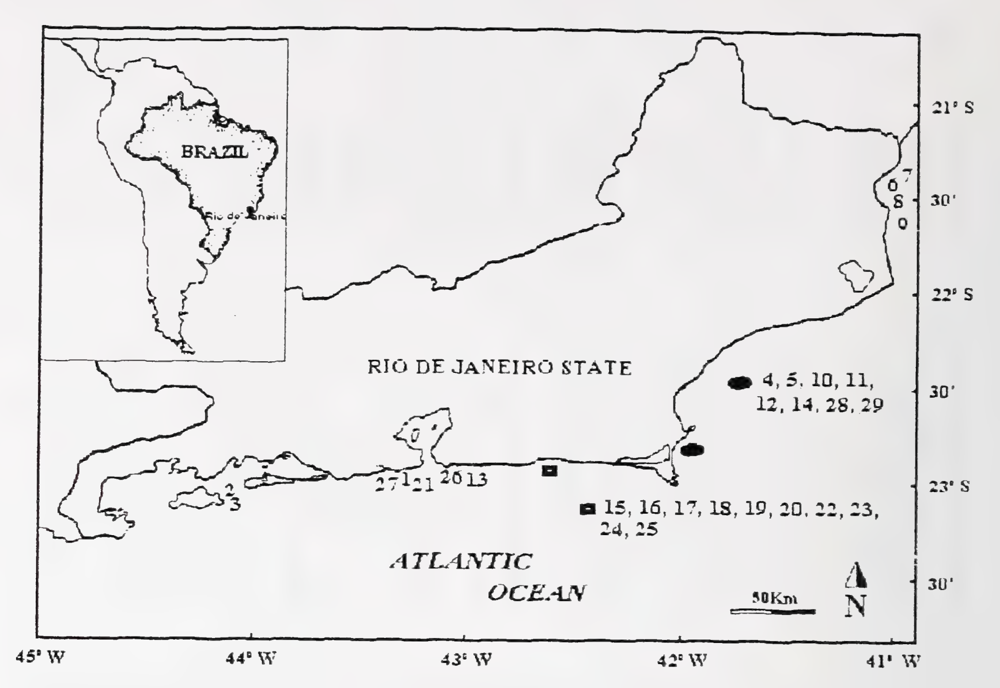


Fig. 1. Sighting locations of killer whales (*Orcinus orca*) along the Rio de Janeiro state coast. Map key refers to table 1.

may also reflect a true killer whale occurrence pattern at the Rio de Janeiro coast. Updwelling conditions present along the Rio de Janeiro coast in summer months lower surface water temperature to 18 °C, or even less.

The resighting interval of 37 days for an individual whale poses some questions on group composition, habitat preferences and distribution patterns. Baird et al. (1992) listed some of the behavioural and ecological differences between transient and resident killer whale populations in the Pacific northwest. According to these authors, the most important differences relate to diet and habitat use. Transient killer whales show small groups sizes (1–15); unpredictable seasonal occurrence and foraging area generally in coastal waters. Our observations suggest some degree of ecological requirements listed for transient killer whales in Baird et al. (1992). Killer whales may visit shallow waters of Rio de Janeiro in search of favorable prey that could include small as well as large whales. Some potential prey are the marine tucuxi (*Sotalia fluviatilis*), the franciscana (*Pontoporia blainvillei*), the rough-toothed dolphin (*Steno bredanensis*), the Atlantic spotted dolphin (*Stenella frontalis*), the bottlenose dolphin (*Tursiops truncatus*), the common dolphins (*Delphinus* spp.) and Bryde's whale (*Balaenoptera edeni*).

However, there is no evidence of feeding by killer whales on marine mammals in our observations. On the other hand, such potential predation pressure on small dolphins could explain why *Sotalia* groups are virtually confined to coastal shallow bays and/or river mouths associated with turbid waters. More recently, Ott and Danilewicz (1996) reported the presence of three franciscanas in the stomach of a stranded female killer whale in southern Brazil. It is also possible that killer whales take advantage of the upwelling conditions on the coast of Rio de Janeiro and may forage on a variety of seasonally abundant sharks, rays, large fish (e. g. *Euthynnus alletteratus* "bonito", *Scomberomorus* spp. "cavala", and *Coryphaena hippurus* "dourado") and cetaceans. At least two

observations were conducted on the presence of rays: it was noted in one case a whale attacking a ray (unidentified species).

These sightings indicate that killer whales, once thought to be rare in shallow coastal waters of southeastern Brazil, may use this habitat seasonally as a foraging ground.

Acknowledgements

We thank A. P. Di Beneditto, R. Ramos, and the photographers E. Fernandes (Petrobras) and A. Branco (Jornal O Globo) for the access to their data. D. E. Sergeant, P. H. Ott, D. Danilewicz, and L. Dalla Rosa kindly commented on the manuscript.

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Buchbesprechung

Qumsiyeh, M. B.: **Mammals of the Holy Land.** Lubbock: Texas Tech University Press 1996. 389 pp., 72 black and white photographs, 43 maps, hard cover. Price $ 35,–. ISBN 0-89672-364-X.

This book deals with the mammals of Israel and the western part of Jordan, i.e., an area between latitudes 29° and 34° N and longitudes 34° and 38° E. The author, born in the Holy Land and presently working at Duke University in the United States, gives a concise introduction into the mammalian fauna of an area in the border zone between Asia and Africa.

After a short introduction and an account of the historical development of mammal research in the Holy Land, the author makes short remarks on the study of mammals in general, deals with "Mammalian evolution and human history", discusses different mammalian adaptations and the interrelationship between mammalian parasites and human health and introduces the reader to the geography and ecology of the Holy Land. After remarks on the zoogeography of mammals and aspects of conservation, the most extensive part of the book from page 59 through 316 deals with a synopsis of the mammals of the Holy Land.

For eight mammalian orders a short introduction is given and a dichotomous key allows the determination of genera within mammalian families. Subsequently, the mammalian species that live in the considered geographical area are described. First the original descriptions and synonyms are cited, followed by a diagnosis. An account of the geographical range of the different species is illustrated by a distribution map. The local status is characterized and information on the biology of the respective species is given. Under the heading "Genetics" information on the karyotype is supplied. The final section "Human interactions" supplies information on names given to species by the local inhabitants, as well as the significance of the mammalian species in rural medicine and folklore. The description of many of the considered species includes black and white photos. The quality of printing of these halftone illustrations is generally poor, i.e., in most cases very dark. This reduces the information drastically that was originally intended by inclusion of the photos.

Following the major part of the book, it continues with short notes on introduced and domesticated mammals, a compilation of scientific terms in a glossary, thirty pages of references and an appendix listing localities with their geographical coordinates. Because of the diffculties in transcription of both Arabic and Hebrew names into English, many localities are represented by more than one name or spelling. Finally, a detailed index of more than 12 pages concludes this book, which will certainly be of great help to those visitors of the Holy Land who are interested in the mammalian fauna of this area.

P. Langer, Gießen

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ISSN 0044-3468 · Z. Säugetierkunde · 64(1999)5 · S. 257-320 · Oktober 1999

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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Z. Säugetierkunde **64** (1999) 257–268

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Roosts, echolocation calls and wing morphology of two phonic types of *Pipistrellus pipistrellus*

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Receipt of Ms. 27. 08. 1997
Acceptance of Ms. 05. 05. 1999

Abstract

Variation in the number of bats in maternity roosts of two phonic types of *P. pipistrellus* was investigated. Also, bats of the two phonic types were caught at maternity roosts, and their wing morphology and echolocation calls studied. 45 kHz *P. pipistrellus* maternity roosts contained significantly fewer bats than 55 kHz *P. pipistrellus* roosts. There was significant variation in mean frequency of maximum energy (FMAXE) of echolocation calls used by bats among roosts of 55 kHz *P. pipistrellus*, but not among roosts of 45 kHz *P. pipistrellus*. However, within each phonic type differences among roosts only accounted for a small proportion of the variation in echolocation call frequency; a much larger proportion was due to differences among individuals. Forearm length, an indicator of body size, was larger in 45 kHz *P. pipistrellus* than in 55 kHz *P. pipistrellus*, but there was no relationship between body size and geographic roost location in either phonic type. Variation in echolocation call frequency was not correlated with body size in either phonic type. Variation in echolocation call frequency among individuals may allow roost members to identify others in their group, but it is more likely to have evolved as a result of other influencing factors. Some variables of wing morphology differed between the two phonic types, but it is not clear how these differences relate to flight performance.

Key words: *Pipistrellus pipistrellus*, cryptic species, ultrasound, body size, ecomorphology

Introduction

Maternity roosts of the vespertilionid bat *Pipistrellus pipistrellus* (Schreber, 1774) are formed from May to July in the British Isles. These maternity roosts are aggregations of mainly adult female bats and their pups (Stebbings 1968; Speakman et al. 1991) and are usually found in buildings (Corbet and Harris 1991). Adult females may occupy a number of different roosts during the year, but are often loyal to the same set of roosts for several years (Thompson 1992). The number of females in roosts of *P. pipistrellus* in the British Isles varies widely from a few bats to over a thousand in some cases (Speakman et al. 1991); up to double that number emerge from roosts when young bats are flying, usually during July.

In this study, we investigated the roosting ecology and wing morphology of *P. pipistrellus* in the British Isles. *P. pipistrellus* exists as two phonic types over much of Europe (Jones and van Parijs 1993). Search-phase echolocation calls (Griffin et al. 1960) of these phonic types have a frequency of maximum energy (FMAXE) at around 55 kHz in one type, and at around 45 kHz in the other. We will refer to the phonic types as 45 kHz *P. pipistrellus* and 55 kHz *P. pipistrellus* throughout this study, though there is now unequivocal evidence that they are cryptic species (Barratt et al. 1997; Barlow

1997; Barlow and Jones 1997 a, b; Barlow et al. 1997; Jones 1997). The nomenclature of *P. pipistrellus* is currently being amended accordingly by the International Commission on Zoological Nomenclature.

There are several benefits to animals living in groups, which may include increased access to resources, information transfer, decreased risk of predation, and increased reproductive success (Hamilton 1971; Ward and Zahavi 1973; Pulliam and Caraco 1984; Brown 1988; Wilkinson, 1992; Speakman et al. 1992; Speakman et al. 1995; Fenton et al. 1994). Roosting communally may also have energetic benefits (Trune and Slobodchikoff 1976; Roverud and Chappell 1991). There are costs, however, of coloniality, including for example increased parasite loads (Brown and Brown 1986; Barclay 1988; Lewis 1996). Optimal colony size will differ according to ecological circumstances. We predicted that the two phonic types of *P. pipistrellus* might have different colony sizes since they show differences in diet (Barlow 1997) and in habitat use (Vaughan et al. 1997 a).

Group cohesion may be achieved by bats if individuals produce individually identifiable communication calls specifically to maintain group coherence or to identify their relatives (e. g. Balcombe 1990; Rasmuson and Barclay 1992; Scherrer and Wilkinson 1993) or their group mates (e. g. Cheney and Seyfarth 1982; Ford 1989; Wilkinson and Boughman 1998). Bat echolocation calls may function in communication (Fenton 1985, 1994). Pearl and Fenton (1996) suggest that echolocation call structure may be colony-specific and used in group recognition, and therefore in the maintenance of group cohesion. There is variation in echolocation call frequency among individual *P. pipistrellus* (Miller and Degn 1981), which could allow individual or colony identification, although individual variation may be caused by sex, or body size effects (Jones 1995).

Bats of the two phonic types of *P. pipistrellus* use separate maternity roosts (Jones and van Parijs 1993). First, we counted and compared the numbers of bats in maternity roosts of the two phonic types. Second, we measured body size, indicated by forearm length, and variables of wing morphology of the phonic types. We also investigated variation in body size with geographical roost location in the two phonic types. Third, we investigated whether variation in echolocation call frequency could be explained at the individual level by correlating with body size, or at the roost level by varying among roosts.

Material and methods

Roost counts

The number of adult bats in maternity roosts of the two phonic types were counted at evening emergence between late May and early July 1992-6. In most cases, time-expanded recordings of echolocation calls were recorded as bats emerged from the roosts, and a Sona-Graph was used to determine the phonic type of the bats. Overlap in the frequency of maximum energy in echolocation calls between phonic types is small (<5%, Jones and van Parijs 1993), and roosts can be ascribed to phonic type unambiguously when large numbers of bats are recorded. For some roosts the heterodyne output of a bat detector (S-25; Ultra Sound Advice, London, UK), tuned first to 45 kHz and then to 55 kHz, was used to determine phonic type. Roost counts were transformed with the square root transformation to achieve normality (Zar 1984). The number of bats in roosts of each phonic type was compared with a t-test.

Bat capture at roosts

Adult female bats were caught with a hand-net during evening emergence at 16 roosts of each of the two phonic types during June 1993–1996. The length of the left forearm was measured to the nearest 0.1 mm with dial callipers, as an index of body size, and a wing tracing was made of the left wing of each captured bat. A magnetic tablet (SummaSketch III, Summagraphics, Fairfield, USA) and software written by Professor J. M. V. Rayner (School of Biological Sciences, University of Bristol) were

used to digitise the wing tracings and morphological variables were measured from them (NORBERG and RAYNER 1987). Variables measured were wingspan (B), total wing area (S), hand-wing area (HWA), hand-wing length (HWL), arm-wing area (AWA), and arm-wing length (AWL); variables calculated were aspect ratio (AR), tip length ratio (TL), tip area ratio (TS), and tip shape index (I).

Each bat was released from the hand in open habitat, and its echolocation call sequence was recorded via the high frequency output of a bat detector (S-25) to a Portable Ultrasound Processor (PUSP; Ultra Sound Advice, London, UK). A 2.2 s sequence of digitised signal (sampled at 448 kHz) was stored in the PUSP and replayed to a Walkman (WM-D6C; Sony, Tokyo, Japan) at one tenth of the original speed. The bat detector (S-25) microphone had a response of ±3 dB from 20–120 kHz; the Walkman had a response of ±3 dB from 40 Hz to 15 kHz. The recordings were analysed by using a Digital Signal Processing Sona-Graph (5500; Kay Elemetrics, Pine Brook, New Jersey, USA; 512 point fast Fourier transform with Hamming window, 400 Hz frequency resolution). The mean frequency containing most energy (FMAXE) of calls produced by each bat was calculated from power spectra of 3–6 echolocation calls. Each roost was considered to be composed of either 45 kHz *P. pipistrellus* or 55 kHz *P. pipistrellus*, on the basis of the mean FMAXE of all bats caught from that roost. Roosts were assigned to 45 kHz *P. pipistrellus* if the roost mean FMAXE was less than 49 kHz, and to 55 kHz *P. pipistrellus* if the roost mean FMAXE was greater than 52 kHz (JONES and VAN PARIJS 1993). This categorisation allowed unambiguous separation of the phonic types, with each phonic type corresponding to the two different genotypes with a sequence divergence of >11% in the cytochrome *b* gene of mitochondrial DNA identified by BARRATT et al. (1997).

Variation in FMAXE of echolocation calls among roosts of each phonic type was investigated by using analysis of variance (ANOVA). Variance component estimates were calculated to determine how much variation in FMAXE was explained by differences among roosts, and how much by differences among individuals (SOKAL and ROHLF 1995). Variables of wing morphology were compared between phonic types with t-tests or Mann Whitney tests. Geographical variation in forearm length, according to roost location, was investigated by using multiple least squares regression analysis on roost latitude and longitude for each phonic type. The relationship between individual forearm length and FMAXE was investigated in the two phonic types.

Results

Roost counts

The number of bats in 33 roosts of 45 kHz *P. pipistrellus* ranged from 20 to 223, with a median of 76 bats. The number of bats in 40 roosts of 55 kHz *P. pipistrellus* ranged from 30 to 650, with a median of 203 bats. There were significantly more bats in 55 kHz *P. pipistrellus* roosts than in 45 kHz *P. pipistrellus* roosts ($t_{71} = 6.15$, $P < 0.001$; Fig. 1).

Echolocation calls

The 16 roosts of each of the two phonic types at which bats were caught are shown in figure 2; between 6 and 20 adult female bats were caught at each roost. Figure 3 shows the distribution of individual FMAXE in the two phonic types. A comparison of FMAXE of echolocation calls found in this study and in previous studies of the two phonic types of *P. pipistrellus* is shown in table 1. In 45 kHz *P. pipistrellus*, there was no significant difference in FMAXE among roosts ($F_{15,165} = 1.66$, NS; Tab. 2). Variance component estimates showed that only 5.5% of the variation in FMAXE was explained by differences among roosts, whereas 94.5% was explained by differences among individuals. In 55 kHz *P. pipistrellus*, there was a significant difference in FMAXE among roosts ($F_{15,204} = 3.45$, $P < 0.00$, Tab. 2). Variance component estimates showed that 15.2% of the variation in FMAXE was explained by differences among roosts, and 84.8% by differences among individuals. Three bats (of 401 recorded) which were assigned to 45 kHz *P. pipistrellus* on the basis of roost mean FMAXE, had FMAXE in the range 52–54 kHz (Fig. 3). These three individuals were therefore not included in further analysis.

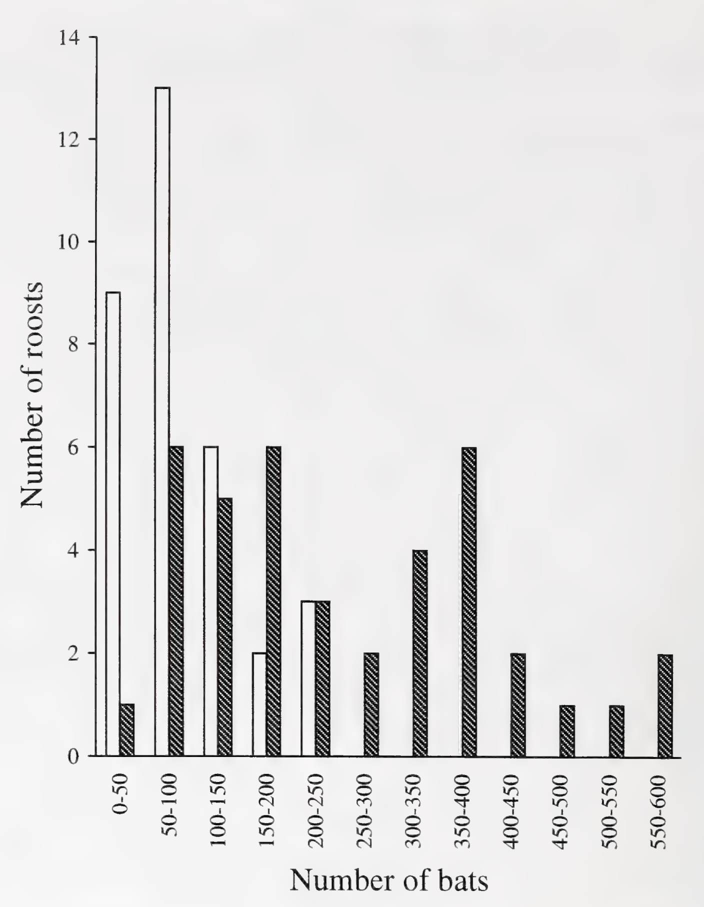


Fig. 1. Histogram showing the frequency distribution of the number of bats in 45 kHz *P. pipistrellus* roosts (white bars) and in 55 kHz *P. pipistrellus* roosts (hatched bars). There were significantly more bats in 55 kHz *P. pipistrellus* roosts than in 45 kHz *P. pipistrellus* roosts.

Wing morphology

There was much overlap in forearm length (mm) between the two phonic types (45 kHz *P. pipistrellus*: mean = 32.0, sd = 0.82, range 29.9–33.9, n = 178; 55 kHz *P. pipistrellus*: mean = 31.7, sd = 0.77, range 29.9–33.7, n = 220; Fig. 4). However, forearm length was significantly longer in 45 kHz *P. pipistrellus* than in 55 kHz *P. pipistrellus* ($t_{396} = 3.87$, $P < 0.001$). Multiple regression analysis of forearm length on two measures of geographical roost location, latitude and longitude, showed that there was no relationship between forearm length and roost location in either 45 kHz *P. pipistrellus* ($r^2 = 0.024$, $F_{2,175} = 2.12$, NS) or 55 kHz *P. pipistrellus* ($r^2 = 0.012$, $F_{2,217} = 1.28$, NS). There was also no correlation between forearm length and FMAXE of echolocation calls in either 45 kHz *P. pipistrellus* ($r_{176} = 0.08$, NS), or 55 kHz *P. pipistrellus* ($r_{218} = -0.05$, NS). The variables B, S, HWA, HWL, AWL, TS, and I were all significantly larger in 45 kHz *P. pipistrellus* than in 55 kHz *P. pipistrellus* (Tab. 3). However, there was much overlap in all these variables between the two phonic types.



Fig. 2. A map of mainland Britain showing the roosts at which bats of the two phonic types of *P. pipistrellus* were caught. Open circles represent 45 kHz *P. pipistrellus* roosts (n = 16); closed circles represent 55 kHz *P. pipistrellus* roosts (n = 16).

Discussion

Wing morphology and echolocation calls

The FMAXE of echolocation calls of the two phonic types of *P. pipistrellus* recorded in this study was similar to that found in previous studies (Jones and van Parijs 1993; Vaughan et al. 1997 b), the two types differing by 8–9 kHz on average. It is unclear whether the three bats (0.75% of total) that were classified as 45 kHz *P. pipistrellus*, but whose FMAXE fell within the range of 55 kHz *P. pipistrellus* were in fact individuals of 45 kHz *P. pipistrellus* with unusually high FMAXE, or were individuals of 55 kHz *P. pipistrellus* in a 45 kHz *P. pipistrellus* roost.

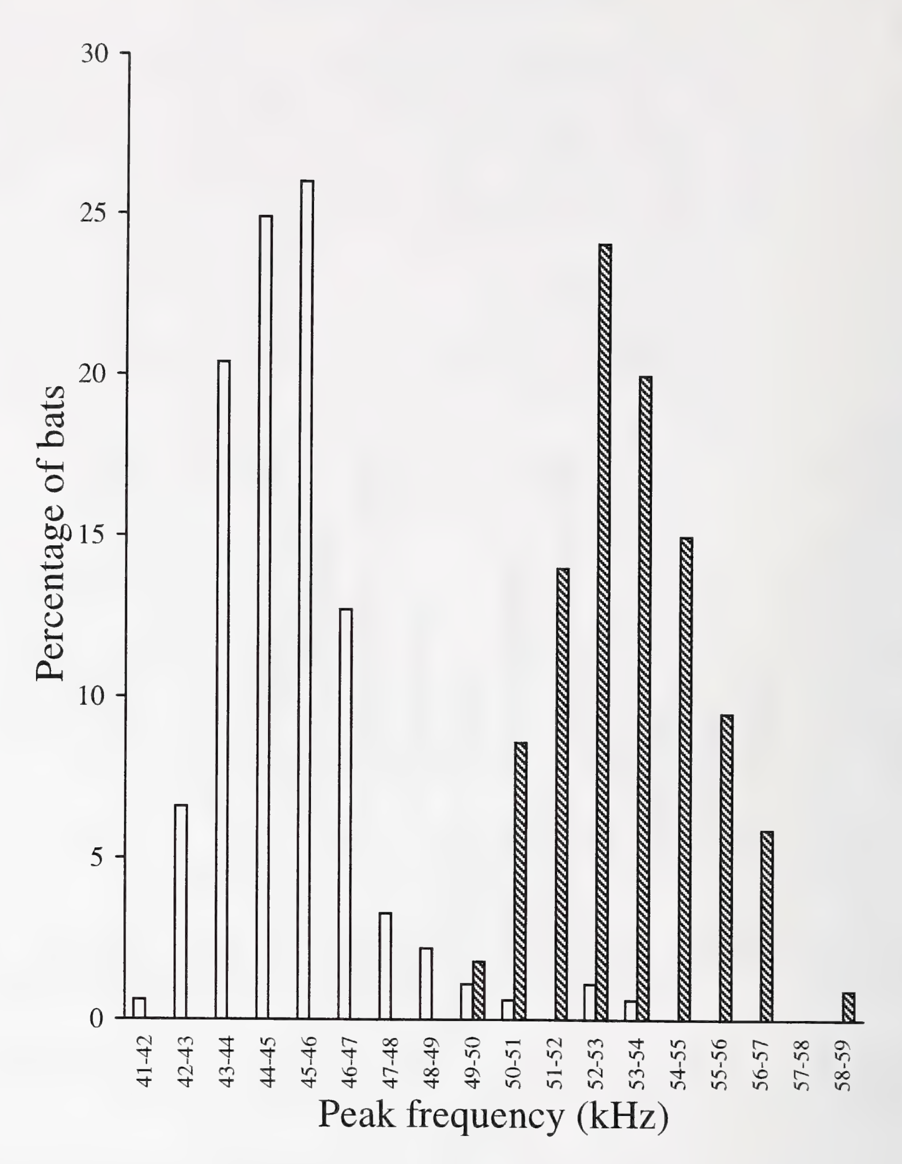


Fig. 3. Histogram showing the percentage distribution of FMAXE (kHz) of echolocation calls of bats of the two phonic types recorded as they were released from the hand. White bars represent the percentage of 45 kHz *P. pipistrellus* in each category (n = 181); hatched bars represent the percentage of 55 kHz *P. pipistrellus* in each category (n = 220).

In some species that produce FM echolocation calls, FMAXE decreases with increasing body size (Jones and Rayner 1991; Jones and Kokurewicz 1994). In several other species, however, FMAXE of echolocation calls is not related to body size (Neuweiler et al. 1987; Jones et al. 1992; Jones and Ransome 1993; Obrist 1995), and no such relationship has been found in *P. pipistrellus* (Jones et al. 1991; Jones and van Parijs 1993). The absence of any relationship between FMAXE of echolocation calls and forearm length in the two phonic types is therefore not unexpected.

Table 1. Echolocation call FMAXE (kHz) of bats of the two phonic types of *P. pipistrellus*. Data are from this study, Jones and van Parijs (1993), and Vaughan et al. (1997b). In the studies by Jones and van Parijs (1993) and Vaughan et al. (1997b), bats were recorded as they emerged from roosts. In this study, bats were recorded as they were released from the hand.

	Mean	sd	Range	n
45 kHz *P. pipistrellus*				
This study	45.1	1.77	41.8–53.0	181
Jones and van Parijs (1993)	46.3	1.97	–	174
Vaughan et al. (1997b)	46.0	1.77	41.6–50.8	60
55 kHz *P. pipistrellus*				
This study	53.2	1.76	49.6–58.0	220
Jones and van Parijs (1993)	55.1	2.62	–	398
Vaughan et al. (1997b)	53.8	1.7	49.2–57.6	59

Table 2. Frequency of maximum energy (FMAXE) of echolocation calls (kHz) and forearm lengths (mm) of bats from 16 roosts of 45 kHz *P. pipistrellus* and 16 roosts of 55 kHz *P. pipistrellus*. Roosts are listed from north to south by latitude in each phonic type.

Roost	FMAXE (kHz)		FA (mm)	
	Mean ± sd	Range	Mean ± sd	n
45 kHz *P. pipistrellus*				
Killiekrankie	46.7 ± 1.90	43.2–50.4	32.0 ± 0.87	14
Bleaton Hallet	45.3 ± 1.70	41.8–48.3	31.7 ± 0.57	18
Earswick	44.9 ± 1.47	42.7–47.6	32.8 ± 0.75	11
Claphouse Fold	44.5 ± 0.97	42.1–45.5	32.3 ± 0.68	9
Stone	44.9 ± 1.23	43.1–47.8	32.0 ± 0.76	18
Newton	44.3 ± 1.73	42.3–48.1	31.6 ± 0.73	9
Llanspyddid	45.0 ± 1.00	42.9–46.7	31.5 ± 0.82	9
Cambridge	45.0 ± 1.76	43.2–49.3	32.1 ± 0.88	10
Woodchester	43.9 ± 1.41	42.7–46.7	31.7 ± 0.61	6
Bwlch	44.2 ± 1.18	42.5–45.9	32.0 ± 0.88	10
Priston	45.2 ± 0.99	43.9–46.8	32.0 ± 0.51	7
Frensham	45.1 ± 1.55	42.7–47.2	31.9 ± 0.57	13
Ditcheat	44.5 ± 0.94	43.6–46.3	32.2 ± 0.97	10
Tracebridge	46.1 ± 1.45	44.9–48.9	31.6 ± 0.65	6
Trendeal	45.3 ± 2.06	42.4–49.0	31.5 ± 0.86	15
Trenowth	45.2 ± 0.66	44.1–46.4	32.3 ± 0.96	16
55 kHz *P. pipistrellus*				
Haddoo	53.6 ± 1.28	51.5–55.9	31.9 ± 0.92	19
Glen O'Dee	53.3 ± 1.87	50.6–56.7	32.0 ± 0.71	20
Larochmore	53.6 ± 1.82	50.0–56.2	31.5 ± 0.82	20
Inchmaggranakhan	55.0 ± 1.80	51.1–58.0	31.8 ± 0.64	14
Bretton	52.4 ± 1.69	49.9–56.1	31.5 ± 0.69	13
Beaumaris	52.6 ± 0.91	50.5–53.4	31.5 ± 0.60	9
Doveridge	52.0 ± 1.38	50.4–54.7	31.4 ± 0.70	18
Bromham	53.6 ± 0.59	52.7–54.5	31.8 ± 0.76	6
Llangors	53.0 ± 1.97	49.7–55.8	31.4 ± 0.86	10
Barrow	53.2 ± 1.57	50.5–56.2	31.7 ± 0.78	18
Winsley	53.4 ± 1.66	51.5–55.7	32.0 ± 0.71	9
Waterham	51.9 ± 1.33	49.6–53.7	31.5 ± 0.65	17
Sheephatch	54.4 ± 1.26	52.5–56.0	32.5 ± 0.43	7
Castle Cary	53.6 ± 1.67	50.9–56.2	31.0 ± 0.73	16
Puckington	53.4 ± 1.34	51.4–55.6	31.9 ± 0.92	9
High Hampton	52.8 ± 2.30	50.0–58.0	31.7 ± 0.58	15

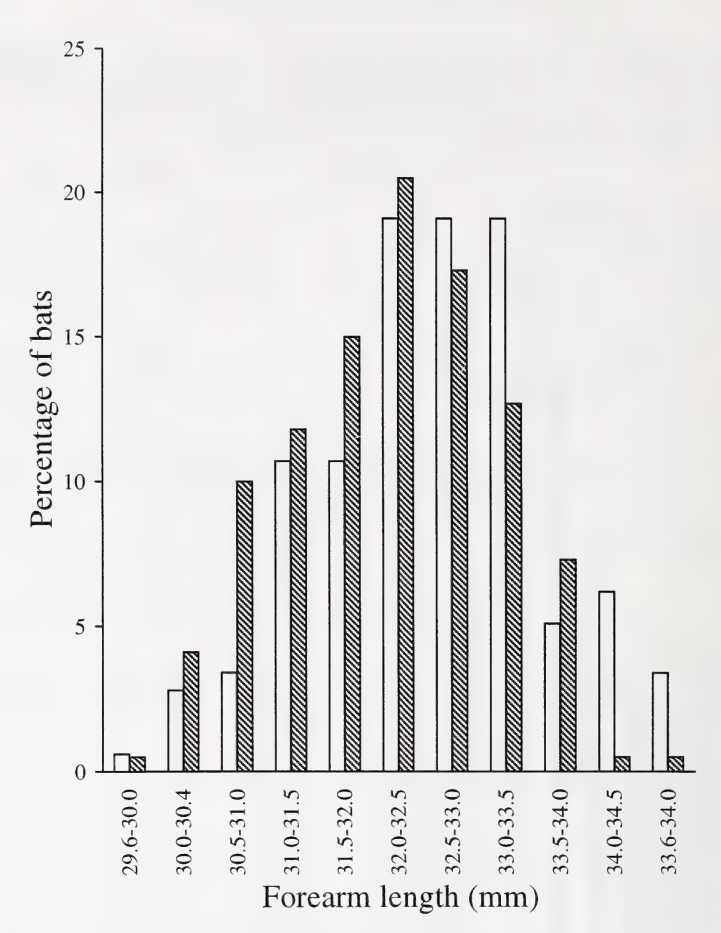


Fig. 4. Histogram showing the percentage distribution of forearm length (mm) of bats of the two phonic types. White bars represent the percentage of 45 kHz *P. pipistrellus* in each category (n = 178); hatched bars represent the percentage of 55 kHz, *P. pipistrellus* in each category (n = 220). Forearm was significantly longer in 45 kHz *P. pipistrellus* than in 55 kHz *P. pipistrellus.*

Table 3. Wing morphology of two phonic types of *P. pipistrellus.* Data are from 226 bats from 16 roosts of 45 kHz *P. pipistrellus* and 253 bats from 16 roosts of 55 kHz, *P. pipistrellus.* Statistics are from t-tests or Mann Whitney tests (W statistic) between phonic types. *P < 0.05, **P < 0.01, ***P < 0.001.

Variable	45 kHz *P. pipistrellus*		55 kHz *P. pipistrellus*		t
	Mean ± sd	range	Mean ± sd	range	
wingspan, B (mm)	217 ± 6.7	200–234	215 ± 7.2	192–232	2.62**
wing area, S (cm^2)	71.1 ± 4.5	57.0–84.4	70.1 ± 5.2	57.1–88.5	2.44*
hand-wing area, HWA (cm^2)	13.9 ± 0.9	10.7–16.1	13.4 ± 1.0	10.4–16.4	5.06***
arm-wing area, AWA (cm^2)	17.5 ± 1.7	13.2–21.9	17.3 ± 1.8	12.9–22.0	1.30
hand-wing length, HWL (mm)	53.5 ± 1.8	48.0–59.0	52.9 ± 0.2	47.0–58.0	3.50***
arm-wing length, AWL (mm)	44.8 ± 2.1	40.0–50.0	44.2 ± 2.4	38.0–50.0	2.78**
aspect ratio, AR	6.62 ± 0.28	5.83–7.43	6.62 ± 0.31	5.57–7.61	0.14
tip area ratio, TS	0.80 ± 0.08	0.63–1.03	0.78 ± 0.07	0.64–1.02	W = 57 144*
tip length ratio, TL	1.20 ± 0.06	1.02–1.39	1.20 ± 0.07	0.98–1.47	W = 61 118
tip shape index, I	2.11 ± 0.7	1.20–6.28	1.94 ± 0.5	1.15–5.63	W = 56 156**

In both phonic types, only a small percentage of the overall variation in FMAXE (around 3 kHz in each phonic type) was attributable to differences among roosts (5.5% in 45 kHz *P. pipistrellus*; 15.2% in 55 kHz *P. pipistrellus*). The small among-roost variation and the large interindividual variation found in FMAXE in both phonic types provide little support for the hypothesis of group recognition by echolocation call frequency suggested by PEARL and FENTON (1996). The results of this study suggest that it is more likely that interindividual variation in FMAXE in the two phonic types of *P. pipistrellus* has evolved as a result of factors not functionally related to group recognition. Whatever the reason for the observed interindividual variation, it may possibly allow recognition among bats in a roost (MASTERS et al. 1995). Odour may be more important in individual recognition in *P. pipistrellus*. Individuals of *P. pipistrellus* can recognise and discriminate between odours of conspecifics, both from their own and from other colonies (DE FANIS and JONES 1995), suggesting that scent cues may be used by individuals in the identification of others, perhaps in conjunction with acoustic cues.

The small but significant difference found in body size, indicated by forearm length, between the two phonic types was in accordance with JONES and VAN PARIJS (1993): 45 kHz *P. pipistrellus* is larger than 55 kHz *P. pipistrellus*. In some vespertilionids including *P. pipistrellus*, body size increases with increasing latitude north (FINDLEY and TRAUT 1970; STEBBINGS 1973; BURNETT 1983; BOGDANOWICZ 1990). STEBBINGS (1973) found that adult female *P. pipistrellus* tended to have longer forearms in the north and east of the British Isles. In this study, however, no such relationship between geographical roost location and forearm length was found in either of the two phonic types. There were small but significant differences between the two phonic types in most of the wing morphology variables measured, suggesting that they may differ in flight performance (NORBERG and RAYNER 1987). ALDRIDGE (1986) showed that even small differences in wing morphology between morphologically similar bat species have significant effects on flight performance. Other studies, however, have found little evidence that small differences in wing morphology between species significantly affect foraging behaviour (e.g. BRIGHAM et al. 1992; SAUNDERS and BARCLAY 1992). We found no difference between the phonic types in aspect ratio (AR), an important parameter for flight efficiency (NORBERG and RAYNER 1987; NORBERG 1994). This is in contradiction to JONES and VAN PARIJS (1993), who found a significant difference in AR between the two phonic types. The larger tip shape index of 45 kHz *P. pipistrellus* suggests that it has more rounded wings than 55 kHz *P. pipistrellus* and may fly more slowly (NORBERG and RAYNER 1987).

In summary, differences in the roosting ecology and wing morphology found in this study between the two phonic types of *P. pipistrellus* corroborate existing evidence that they are cryptic species. Within each phonic type, variation in echolocation call frequency was small at the roost level and greater at the individual level, but could not be accounted for by body size variation.

Acknowledgements

KATE E. BARLOW thanks members of local Bat Groups of the Bat Conservation Trust in the U.K. who took me to pipistrelle roosts, helped to catch bats and to count roosts, and put me up in their homes. Roost owners kindly allowed me to work on their property. The work was carried out under licence from English Nature, Scottish Natural Heritage and Countryside Council for Wales. Professor J. M. V. RAYNER allowed me the use of his digitising software. Funding was from N.E.R.C.

Zusammenfassung

Quartiere, Echoortungslaute und Flügelmorphologie von zwei akustischen Typen von Pipistrellus pipistrellus

Bei zwei akustischen Typen von *Pipistrellus pipistrellus* wurden Unterschiede in der Zahl der Tiere in den Wochenstubenquartieren, in der Flügelmorphologie und bei den Ultraschallrufen untersucht. In Wochenstubenquartieren der 45 kHz *P. pipistrellus* waren signifikant weniger Tiere als in den Quartieren der 55 kHz *P. pipistrellus.* Die mittlere Hauptfrequenz der Ultraschallrufe variierte zwischen den Quartieren der 55 kHz *P. pipistrellus*; bei den 45 kHz *P. pipistrellus* wurde kein solcher Unterschied gefunden. Diese Unterschiede erklärten jedoch immer nur einen kleinen Teil der Variabilität in der Hauptfrequenz der Ultraschallrufe, ein weit größerer Teil wurde durch Unterschiede zwischen den Individuen erklärt. Bei den 45 kHz *P. pipistrellus* war die mittlere Unterarmlänge ein Maß für die Körpergröße, größer als bei den 55 kHz *P. pipistrellus.* Bei beiden Gruppen konnte jedoch kein Zusammenhang zwischen Körpergröße und geographischer Lage der Quartiere festgestellt werden. Bei beiden Gruppen waren die individuellen Unterschiede in der Hauptfrequenz der Ultraschallrufe nicht mit der Körpergröße korreliert. Individuelle Unterschiede in der Frequenz der Ultraschallrufe könnten der Erkennung anderer Koloniemitglieder dienen, wahrscheinlicher ist jedoch eine evolutive Entfaltung bedingt durch andere Faktoren. Verschiedene Merkmale der Flügelmorphologie unterschieden sich bei den Gruppen; es ist jedoch noch unklar, wie diese die Flugweise bestimmen.

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Z. Säugetierkunde **64** (1999) 269–276

http://www.urbanfischer.de/journals/saeugetier



Physical and population parameters of Eurasian badgers (*Meles meles* L.) from Mediterranean Spain

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Reiceipt of Ms. 20. 10. 1998
Acceptance of Ms. 05. 05. 1999

Abstract

Biometry, reproduction, and density of the Eurasian badger (*Meles meles*) population living in the Doñana area, Mediterranean Spain, were investigated. These badgers were smaller, lighter, and less sexually dimorphic than those from any other region of this widely distributed species. There was no significant seasonal variation in body mass. Most of the births occurred in January. Reproduction occurred once a year in 67% of the territories. All females older than two years had bred at least once; and 65% bred in the calendar year of capture. Badger densities ranged from 0.23 to 0.67 individuals/km^2. These densities are between five and 125 times lower than that of populations inhabiting temperate ecosystems, where badgers feed on earthworms. Biometric and reproductive parameters of this population fit into the clinal variation found across Europe, where badgers are smaller and breed earlier to the south. Low densities can be explained as a functional response to the low productivity of Mediterranean areas and can also be expected for many other parts of the species' distribution area, where earthworms are not the staple food.

Key words: *Meles meles*, biometry, density, reproduction, Mediterranean areas

Introduction

Mediterranean environments are in some ways different from those found in Eurasian temperate landscapes. Differences include physical environmental characteristics (temperature, humidity), type and structure of vegetation (evergreen sclerophyllous scrubland), prey availability (abundant beetles, reptiles, and rabbits), and strong seasonal patterns (mild winters which are considered the 'good' seasons, and extremely dry and hot summers which are the 'bad' ones; di Castri and Mooney 1973; Delibes 1975). Badgers inhabiting the Iberian Peninsula have been described as *Meles meles marianensis* Graells, 1897, however the only feature used in the description of this subspecies was the paler colour on back and flanks (Long and Killingley 1983). Nowadays no validation of this taxon exists, or knowledge about differences with other badger populations (Long and Killingley 1983). The IUCN conservation status of badgers in Spain is insufficiently known (Blanco and Gonzalez 1992), as in other Mediterranean countries (Griffiths and Thomas 1997). Griffiths and Thomas (1997) remarked on the importance of undertaking research on Mediterranean badgers for the future conservation of the species. In order to improve the scarce knowledge about Mediterranean badgers, we studied biometry, reproduction, and density of animals living in a Mediterranean area of Spain.

0044-3468/99/64/05–269 $ 12.00/0

Material and methods

Study area and animals

Animals came from an area of about 1000 km^2, in the SW corner of the Iberian Peninsula (~37°N, 6°30′W). Part of this area is protected by Doñana National and Natural Parks. It has a Mediterranean climate with Atlantic influence (mild wet winters and hot dry summers). Vegetation inside the protected areas is dominated by natural Mediterranean scrubland (*Halimium* spp., *Cistus* spp., *Pistacia lentiscus*, *Rosmarinus officinalis*), degraded cork oak woods (*Quercus suber*), marshland, sand dunes, and pine plantations (*Pinus pinea*); and by pine and eucalyptus (*Eucalyptus* spp.) plantations elsewhere.

We distinguished between three badger age classes: cubs – those with milk teeth or changing to permanent (until 16 weeks old); yearlings – between 16 weeks and two years (24 months old), and adults – two years or older (Neal and Cheeseman 1996). The first two age classes were determined by body size and tooth characteristics (milk teeth, or newly emerged permanent teeth). Adults and some yearlings (those with permanent teeth) were determined by counts of cementum annuli in premolars (Klevezal 1996). This last technique proved accurate in our study area, not only with marked badgers of known age, but also with other carnivore species (Zapata et al. 1995, 1997).

Biometry

Between 1983 and 1998 we measured a total of 78 individual badgers, which were live trapped (N = 75) or found dead (N = 3). Trapped animals were permanently marked with a tattoo or with a microchip. In case of recaptures, we used only the measurements recorded at first. The following data were taken: body weight (BW, precision 100 g); head-body length (HB), from the tip of the snout to the dorsal edge of the perineum; tail length (TL), from the dorsal edge of the perineum to the tip of the tail, excluding fur; hindfoot length (HF), from the edge of the calcaneus to the tip of the third phalange; ear length (EL), from the base of the tragus to the tip of the pinna, excluding hair; and hilt (HI), from the top of the shoulder-blade to the end of the foreleg, excluding hand. Lengths were in mm and measured on the left side of the animal. We used only adult animals in the analysis, and excluded also the weight of pregnant females. Variations in body weight between sex classes and seasons were analysed with a fixed effect two way analysis of variance (ANOVA). All other measurements were analysed in relation to sex, using a multivariate analysis of variance (MANOVA). Normality and equality of variances were assessed through Kolmogorov-Smirnov and Levene tests (Zar 1996). Sexual dimorphism was also evaluated using the index male measurement/female measurement (Moors 1980; Travaini and Delibes 1995).

Reproduction

Data on reproduction were obtained from live trapped and dead animals, and from the monitoring of radiotagged individuals (see Density). Birth dates were estimated (to the nearest month) based on teeth eruption patterns of cubs; by the state of pregnancy following Neal and Cheeseman (1996); and by behavioural changes in radiotagged females, for whom cub presence was later confirmed. We considered that a female had bred if she was pregnant or lactating, or if she had black placental scars in the uterus (Page et al. 1994; Woodroffe 1995; Woodroffe and Macdonald 1995 a, b). Females with extended teats were considered to have bred previously. In males we distinguished individuals with abdominal testes from those with descended testes (Woodroffe and Macdonald 1995 a; Woodroffe et al. 1997).

Density

Radio-tracking was the only accurate way of estimating density, since the difficulties in trapping badgers (about 450 night-traps for capturing a single animal, Revilla 1998) did not allow the use of capture–re-capture techniques. We estimated density in two different populations in the Doñana area.

Animals from the population in the Coto del Rey zone preyed mainly on rabbit kittens (Fedriani et al. 1998; Revilla 1998), while in the Reserva Biologica zone, the population had no staple food (Martin et al. 1995; Revilla 1998). Between 1994 and 1997 we radio-tagged 17 animals in Coto del Rey, from five territories, and in 1997 we marked three females, from three territories in the Reserva Biologica. Territories were determined by radio-tracking (Revilla 1998).

We followed the density estimation approach of Mclellan (1989), estimating density as a function of the time that each radiotagged animal spent in a fixed area within each population (Mclellan 1989). These areas were defined as the minimum convex polygon (MCP) of the locations of all badger captures in Coto del Rey (30 captures, MCP of 7.73 km^2, maximum span of 4096 m); and of all the winter 1997 trapping stations in the Reserva Biologica (91 stations, MCP of 6.87 km^2, maximum span 4205 m). Time periods considered for estimation were calendar years. By using this method we assumed that all animals using these areas are known (Mclellan 1989). The minimum number of animals living in each territory which overlapped with the areas of density estimation was calculated using sighting information and track censuses. Track censuses were conducted in all territories at least once a year (except in 1994) on previously swept sandy roads (in order to erase old tracks, Travaini 1994). The very high density of roads and fire-breaks at both areas allows the identification of the route of a foraging badger just with its tracks on sand (Revilla 1998). All radiotagged badgers were continuously tracked during the night preceding the track census, in order to assign their movement routes to the footprint trails (see Revilla 1998). The results were compared with data obtained using sighting information (both during the night and during sett observations) and tracks around setts (only in the case of young animals). The minimum number of marked plus unmarked individuals was considered as the number of animals using the areas of density estimation. The contribution of every marked animal to the final density was related to the number of days it was known to be present in the area (i. e. only while living in the area). The contribution to the final density of unmarked animals was assumed to be the same as that of other marked individuals from the same territory and period (Maclellan 1989). We made two density estimations, one considering all animals (young animals were assumed to add density from the 1st of March), the other considering individuals older than one year (for more details, see Maclellan 1989; Revilla 1998).

Results

Biometry

Males were slightly heavier and larger than females (Table 1), but the results of the ANOVA for weight did not show any significant difference between sexes ($F(1,63) = 0.72$, $P = 0.401$), seasons ($F(3,63) = 2.10$, $P = 0.890$) or their interaction ($F(2,63) = 2.81$, $P = 0.068$). The remaining measurements showed no significant differences between the sexes (MANOVA $F(5,56) = 1.49$, Wilk's Lambda $P = 0.206$, Tab. 1). The mean index of sexual dimorphism was 1.038 ($SE = 0.008$, $N = 6$), ranging between 1.07 for the weight and 1.02 for ear and tail lengths.

Reproduction

Eight of 11 (73%) registered births were in January, two in December, and one in November. From 1994 to 1997 we monitored reproduction using radiotracking at up to five different territories, totalling 18 year-territory. We confirmed reproduction in ten of them (67%), it was probable in one (6%), and did not occur in four (27%). In the three remaining we could neither confirm nor deny reproduction. Information on litter size was scarce. We registered two foetuses in a pregnant female and three placental scars in another as counts of cubs at birth. A road-casualty female (August 1996) had three unimplanted blastocysts in the uterus, which can be interpreted as a sign of delayed implantation. All females older than two years had bred ($N = 19$), while only one from five 2-year-old animals had bred. Sixty-five percent of the females older than two years bred in the calendar year of capture ($N = 17$). All captured males of two years or older had scrotal

Table 1. Mean values, standard deviation (SD), range and number of measured animals (N) for body weight (BW), head-body length (HB), tail length (TL), hilt (HI), ear length (EL), and hindfoot length (HF), of Eurasian badgers, *Meles meles*, from a Spanish Mediterranean population. Lengths are in mm and mass in g.

	Males				Females			
	mean	range	SD	N	mean	range	SD	N
BW	7333	5850–9300	921.5	23	6884	4800–9200	1086.19	40
HB	680.9	582–750	41.10	22	661.2	592–750	39.77	39
TL	160.9	132–180	13.95	22	158.2	114–200	14.86	39
HI	303.0	247–345	24.91	22	287.3	228–315	19.06	38
EL	45.0	34–50	3.39	21	44.2	39–51	2.82	35
HF	104.8	92–115	4.89	22	101.8	88–120	5.75	39

testes (N = 10). Three out of four yearlings also had descended testes (if assumed born in January, two were 14- and one 17-months old). The fourth (14-months old) had abdominal testes. In two young (9- and 11-months old) they were undescended.

Density

In Coto del Rey, the average number of animals inside the trapping area was 10.25 (SE = 1.10, range 9–13), of which, on average, 65% were radio-marked (SE = 0.12, range 44–88%). Average annual density (between 1994 and 1997) was 0.85 individuals/km^2 (SE = 0.08, range 0.73–1.07) considering all the animals, and of 0.67 individuals/km^2 (SE = 0.05, range 0.57–0.74), excluding the animals born every year. In the Reserva Biologica, badger density in 1997 was 0.28 and 0.23 individuals/km^2 (including and excluding yearlings, respectively), of which three (38%) were radio-marked.

Discussion

Biometry

To the best of our knowledge, Eurasian badgers in the Doñana area are smaller than in any other area studied. Average weights were 1.3–1.8 and 1.2–1.7 times larger in the British Isles and central Europe than in Doñana (for males and females, respectively; Kruuk and Parish 1983; Lüps and Wandeler 1993; Neal and Cheeseman 1996; Rogers et al. 1997 a). Doñana badgers were also lighter than badgers from Huesca, north of Spain (Lüps and Wandeler 1993). Head-body length was 1.1 and 1.21 times larger (respectively for both sexes) in British and German animals than Doñana badgers (Lüps and Wandeler 1993; Neal and Cheeseman 1996).

Smaller animals can be expected in populations where densities are close to the carrying capacity (Rogers et al.1997 a), but as human-induced mortality is very important in the Doñana area (Revilla and Palomares 1996) this density-dependent size constraint does not seem to be the main reason for the small size. Bergmann's rule predicts that, for a given homeotherm species, individuals will be larger when living at lower mean temperatures; thus, body size of homeotherms is correlated to mean ambient temperature, and therefore to latitude (Margalef 1974; Mayr 1956; but see Geist 1987). Also, animals from populations living in less productive areas are expected to be smaller, as absolute values of maintenance cost and food requirements are reduced (both very important for survival during food stress periods). This has been shown by Kruuk and Parish (1985) in

a badger population where weight of the animals in spring and early summer was lighter after a diminution in the main prey availability (earthworms). The Doñana area is poor for badgers in comparison with areas where earthworms are the staple food. Both nutritional factors and Bergmann's rule seem plausible for explaining body size differences, which in turn fit into the clinal variation of body size across Europe, with smaller animals to the south (LYNCH 1993; NEAL and CHESEEMAN 1996).

There were no significant seasonal variations in body weight. In northern populations, badgers have to spend winters with scarce trophic resources. The negative energetic balance produced by scarcity and low temperatures results in an activity reduction and weight loss (FOWLER and RACEY 1988). Winter in non-mountainous Mediterranean areas is rainy and mild with plentiful resources. Badgers in Doñana fed on rabbit kittens during winter (MARTIN et al. 1995) and consequently there is not an adaptative advantage for weight gain in autumn, as in northern populations (NEAL and CHEESEMAN 1996).

Males were not significantly larger than females. In other populations, sexual dimorphism is higher, for example, sexual dimorphism index for body mass was 1.15 in Great Britain and Japan, and 1.16 in Germany and The Netherlands (data from LÜPS and WANDELER 1993; KANEKO et al. 1996; NEAL and CHEESEMAN 1996). One of the hypothesis explaining the sexual dimorphism in mustelids (for a review, see DAYAN and SIMBERLOFF 1996; KING 1989) states that it is a result of sexual competition between males of polygynous species (MOORS 1980; HEDRICK and TEMELES 1989; SHINE 1989). This could suggest that a smaller difference between badger sexes might be related to a greater trend to monogamy (KLEIMAN 1977). In high density populations there is usually only one female breeding per year and territory, but cases where 2 or even 3 females breed are not rare (WOODROFFE and MACDONALD 1993). In Doñana, there was no single case of double or triple births in the same territory (REVILLA 1998; RODRÍGUEZ et al. 1995). This could support the existence of a more strict monogamy in the studied population.

Reproduction

Our results are in accordance with the general trend towards earlier birth dates in the more southerly European populations (NEAL and CHEESEMAN 1996). In Doñana we estimated the average birth date to be within the first week of January whereas in southwest France it is 31 January; in southwest England 7 February; early March in Scotland, Germany, and Sweden and, late March in Russia (NEAL and CHEESEMAN 1996). We did not detect multiple births within a territory and reproduction occurred or most probably occurred in only 73% of controlled territories, which means that in 27% of territories there was no cub recruitment. Of adult females captured (older than two years), 65% bred the year of capture. This is much higher than the 20–40% found by ROGERS et al. (1997 a) in a high density population; but similar to the 73% of breeding females 5 years or older (which are the group dominants, ROGERS et al. 1997 a). Despite the small sample size and potentially large range of error in our estimations, the number of cubs and the year of the first reproduction were similar to other studied populations (AHNLUND 1980; CANIVENC 1966; PAGE et al. 1994)

Density

It is assumed that density in the Reserva Biologica is the lowest ever recorded. This area, composed of stabilised dunes and pine plantations, is adjacent to an area dominated by Mediterranean scrubland where RODRÍGUEZ et al. (1995) recorded badgers at 0.5 individuals/km^2. Based on rabbit abundance (MARTIN et al. 1995; RODRÍGUEZ et al. 1995) our density should be expected to be lower than that calculated by RODRÍGUEZ et al. (1995) because rabbits are more abundant in Mediterranean scrubland (PALOMARES et

al. 1996). In Coto del Rey, badger density was 3.5 times larger than in the Reserva Biologica, and rabbit densities were up to 25 times higher (REVILLA 1998). However, the Reserva Biologica population does not rely on rabbits but on a diversity of food resources, and thus density should be related to the abundance and spatial distribution of these resources, not only to rabbits (KRUUK 1978; MACDONALD 1983; WOODROFFE and MACDONALD 1993). Densities in these Mediterranean populations are 5 to 125 times smaller than those in Eurasian temperate ecosystems (WOODROFFE and MACDONALD 1993), where earthworms form the main part of the diet (they represent only secondary prey in Mediterranean areas; IBAÑEZ and IBAÑEZ 1977; KRUUK, 1989; MARTÍN et al. 1995; PIGOZZI 1988; RODRÍGUEZ and DELIBES 1992; REVILLA 1998). The wide variation in badger densities can be seen as a gradient of functional responses to the diverse carrying capacity of landscapes, with the highest found at Eurosiberian temperate areas, as stated by ROGERS et al. (1997 b). Carrying capacity follows the availability of earthworms through Europe, fluctuating according to differences in annual rainfall and on any other main resource, such as rabbits. Variations in this and other population parameters can be expected for many other areas of the species distribution (boreal forests, mountainous areas, arid areas, and steppes of Asia) where earthworms are not the staple resource (ROPER and MICKEVICIUS 1995).

Eurasian badgers living in this Mediterranean area are different from central European populations and thus their management and conservation needs should be considered separately. To determine the right management and conservation measures, further research is necessary on Mediterranean populations focussing on taxonomic status (GRIFFITHS and THOMAS 1997), abundance and distribution (BLANCO and GONZÁLEZ 1992) and behavioural ecology (REVILLA 1998).

Acknowledgements

The authors would like to acknowledge J. AYALA J. CALZADA, J. M. FEDRIANI, P. FERRERAS, R. LAFFITE, and R. MARTÍN, for trapping some of the animals. CLAIRE SEYMOUR and GUYONNE JANSS greatly improved the English. S. T. WIEGAN kindly reviewed and translated the Zusammenfassung. ER had a predoctoral grant from the Spanish Ministry of Education and Culture. This study was partially financed by the Spanish CAICYT and DGICYT (project numbers 944, PB87-0405, PB90-1018, PB94-0480, and PB97-1163) and sponsored by Rover España.

Zusammenfassung

Physische und demographische Parameter des Eurasischen Dachses (Meles meles L.) im mediterranen Spanien

Es werden Informationen über Biometrie, Reproduktion und Populationsdichten einer Population von Dachsen dem mediterranen Spanien vorgestellt. Die Dachse waren im Vergleich zu anderen untersuchten Populationen kleiner, leichter und sexuell weniger dimorph. Es konnten keine signifikanten jahreszeitlich bedingten Gewichtsunterschiede festgestellt werden. Die meisten Geburten wurden im Januar beobachtet; in 67% der kontrollierten Territorien trat ein Wurf pro Jahr auf und alle Weibchen über 2 Jahre hatten Junge (wobei 65% der Weibchen im Jahr des Fangs setzten). Die Populationsdichte schwankte zwischen 0,23 und 0,67 Individuen/km^2, für die geringsten und am höchsten produktiven Zonen des Untersuchungsgebietes. Diese Werte sind etwa 5 bis 125fach kleiner als Dichten von Dachspopulationen in Ökosystemen gemäßigten Klimas. Die biometrischen und reproduktiven Parameter fügen sich in eine europäische Kline ein. Die geringen Dichten können als funktionelle Antwort auf die unterschiedlichen trophischen Ressourcen mediterraner Populationen erklärt werden. Ähnlich geringe Dichten sind auch für viele andere Dachspopulationen zu erwarten, bei denen Regenwürmer keine Hauptnahrungsquelle sind.

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Z. Säugetierkunde **64** (1999) 277–284
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Intrageneric comparisons in urine-concentrating capacity and renal morphology among three species of *Akodon* from different geographic rainfall regimens

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Receipt of Ms. 09. 11. 1998
Acceptance of Ms. 18. 03. 1999

Abstract

Urine-concentrating capacity and renal morphology were examined for *Akodon azarae*, *A. iniscatus* and *A. cursor* from different geographic rainfall regimens. *A. azarae* and *A. cursor* rejected sodium chloride solution above 0.45 M, whereas *A. iniscatus* did not. *A. azarae* and *A. iniscatus* may concentrate urine to similar osmolarity values. These values were higher than those observed for *A. cursor*. Percent medullary thickness of the kidney for *Akodon* was related to both geographic rainfall regimens and urine osmolarity.

Key words: *Akodon* species, urine osmolarity, renal morphology

Introduction

Water is the primary constituent of animals. Mammals, particularly those adapted to arid habitats, can minimise their urinary water loss due to the fact that their kidneys can produce urine that is significantly more concentrated than their plasma (Brooker and Withers 1994). In mammals, adaptive radiation into new environments may involve both physiological and structural adaptations of the kidney. Hence, interspecific variation in these characteristics may represent adaptive responses to habitat differences in water availability.

Urine-concentrating ability, and consequently the ability to conserve water have been evaluated in many morphological and functional studies on the mammalian kidney. These data have been correlated, in many instances, with water availability and habitat distribution. One example is given by an earlier study performed by Sperber (1944) after examining species representing most mammalian orders, highlighting the relationship between mammal distribution related to climatic factors and their ability to concentrate urine throughout renal morphology. Later on, Schmidt-Nielsen and O'Dell (1961), by studying several mammalian species, found a positive correlation between the relative medullary thickness (RMT; Sperber 1944) and maximum urine osmolality. These studies have been followed by countless others, exploring the relationship between urine-concentrating ability and RMT in hundreds of species of mammals (e.g. Hewitt 1981; Dunson and Lazell 1982; Lawler and Geluso 1986; Beuchat 1990b; Beuchat 1996). Other structural indices have been used to show the relationship between the relative size of the renal medulla and the capacity to concentrate urine: ratio of medullary to cortical thickness (M/C; Geluso 1978), percent medullary thickness (PMT; Heisinger and Breitenbach 1969), relative me-

dullary area (RMA; BROWNFIELD and WUNDER 1976; HEWITT 1981) and percent medullary area (PMA; SCHMID 1972). Nevertheless, the above-mentioned indices must be carefully employed since recent studies on renal morphology have established some limitations in regards to their utilisation. Thus, studies performed by BROOKER and WITHERS (1994), have concluded that for marsupials, only those indices representing relative medullary lenght of the kidneys were correlated to climatic factors, whereas those representing medullary area were not. Moreover, BEUCHAT (1996) found that the relationship between thickness of the medulla and concentrating ability is neither proportional nor direct.

Sigmodontinae rodents are abundant in many dry areas of South America, but few studies on their physiological adaptations have been published (MARES 1975; 1977 a; 1977 b; 1977 c; CORTÉS et al. 1988).

Akodon is a polytypic genus that had a rapid adaptive radiation in the earliest Pliocene (5.67 M. y. B. P.; APFELBAUM and REIG 1989) and was distrubuted in South America from humid to semiarid regions with less than 200 mm precipitation per year. Hence, it is an interesting model for studying intrageneric differences in kidney function and structure that could arise as a consequence of selection pressures imposed by environmental constraints.

The aim of this study was to analyse the intrageneric pattern in urine-concentrating capacity and renal morphology of *A. azarae*, *A. cursor*, and *A. iniscatus* that could be the result of adaptive responses to habitats with different mean yearly rainfall.

Material and methods

Experimental animals

Animals of both sexes were collected using Sherman live traps. Thirty four individuals of *Akodon azarae* were captured at Necochea, Buenos Aires Province (38°29′ S, 58°50′ W; rainfall average: 830 mm.year^{-1}; Pampeana biogeographic province; CABRERA and WILLINK 1973). *A. azarae* is a mouse of moderate size (25 g body mass), strongly associated to natural grassland, particularly to open vegetation formations (BONAVENTURA 1992; REDFORD and EISENBERG 1992). This species, which is the more representative rodent species of the pampa's grasslands, is found from southern Brazil to central Argentina (REDFORD and EISENBERG 1992).

Thirty six individuals of *Akodon iniscatus*, which is a small size mouse (20 g body mass), were captured at Puerto Madryn, Chubut Province (42°77′ S, 65°82′ W; rainfall average 198 mm.year^{-1}; Patagónica biogeographic province). Captured mice were associated with vegetated coastal dunes with scarce availability to water. Distribution of this species also includes the xeric Monte and southern Espinal biogeographic provinces (CABRERA and WILLINK 1973; REDFORD and EISENBERG 1992).

Thirty five individuals of *Akodon cursor* were captured at Posadas, Misiones Province (27°22′ S, 55°58′ W; rainfall average 1 604 mm.year^{-1}; Paranense biogeographic province; CABRERA and WILLINK 1973; REDFORD and EISENBERG 1992). This species, which is a medium size mouse (40 g body mass), is distributed in southern and central Brazil, Uruguay, Paraguay, and northeastern Argentina. At Misiones province it is found in most habitats but prefers flat and less moist areas (REDFORD and EISENBERG 1992).

Climatic data records were obtained from the Meteorological Service of the Argentine Air Force. Only adult animals that maintained or gained body weight in the laboratry were used.

Laboratory conditions

Captured mice were carried to the laboratory and housed individually in animal cages (30 × 22 × 15 cm). Wood shavings and cotton for nesting material were placed on cage floors. All animals were maintained under a natural photoperiod (10L : 14D). Temperature ranged from 18 to 25 °C and relative humidity ranged from 50 to 80 %. Animals were fed with dehydrated pellets ad libitum (composition: minimum protein = 21 %; maximum fiber = 4.5 %; minimum fat = 8 %; average calcium = 1.8 %; phosphorous = 1.1 %; maximum ashes = 8 %). Tap water was provided ad libitum.

Salt-water regimen

Tap water and sodium chloride, prepared in distilled water at different concentrations (0.05, 0.15, 0.25, 0.35, 0.45, 1 and 1.5 M), was offered as a drinking source. To measure consumption, a saline solution was provided during 24 h in inverted graduated glass Erlenmeyer, L-shaped drinking tubes, from which animals rapidly learned to drink. An additional inverted Erlenmeyer was placed near the cage to measure evaporation, which proved to be negligible. Once the Erlenmeyer with saline solution was removed, individuals were deprived of food and water and placed in a urine collection apparatus.

Urine collection

Urine was collected in glass vials containing mineral oil by using a collecting apparatus similar to that described by Drozdz (1975). Urine samples were collected for a total period of 14 h, after which saline solutions were removed and frozen at –20 °C for analysis. Urine samples were discarded when contaminated by fecal material.

Urinalyses

Urine was analysed for total osmolarity measured with an Advanced 3MO osmometer. For evaluating urine-concentration capacity, urine data were analysed as follows: (1) for the whole rank of saline solutions offered (tap water to 1.5 M NaCl) and (2) grouping the data into two categories: low salt concentration (tap water to 0.25 M Na Cl) and high salt concentration (0.35 to 1.5 M NaCl). The latter procedure was performed to mitigate the potential effect of the low number of individuals due to animal supply limitations. ANOVA was used to test the null hypothesis of no effect of saline solution treatments over urine osmolarity. Tukey's test a posteriori was used to identify differences between treatments. T test was used to test the null hypothesis of no effect of saline solution treatments grouped in low or high salt concentration categories over urine osmolarity.

Renal index (PMT)

Data on renal structure (relative size of the renal medulla) was collected as an ancillary measure of urine-concentrating capacity. Within 2 weeks following urine collection, animals were sacrificed by ether inhalation. Fresh kidneys were removed and fixed in 10 % formaline. The kidney tissue was dehydrated and embedded in paraffin wax using standard histological techniques. Serial sagittal sections were cut at 10 µm, and stained with heamatoxylin and eosin. The thicknesses of the cortical and medullary regions were measured to the nearest 0.1 mm with the aid of an ocular micrometer. For each kidney, percent medullary thickness (PMT) was determined by dividing the medullary thickness by the combined thickness of both regions (Heisinger and Breitenbach 1969). A mean of 10 measured PMT values was determined for each specimen. ANOVA was used to test the null hypothesis of no differences in relative medullary thickness (PMT) of the kidney among species. Tukey's test a posteriori was used to identify differences between species.

Results

Fluid consumption

Above 0.25 M of saline solution *Akodon iniscatus* and *A. cursor* decreased their fluid consumption as saline concentration increased, whereas in *A. azarae* it was above 0.35 M. Furthermore, *A. iniscatus* drank saline solutions up to 1.5 M, whereas *A. azarae* and *A. cursor* rejected saline solutions above 0.45 M (Fig. 1).

Urinalyses

Akodon iniscatus and *A. azarae* reached a similar urine osmolarity value (≈ 3 500 mOsmol, ANOVA, $F = 147.9$, $n = 9$, d. f. = 2, Tukey's test, $P > 0.05$). These values were higher

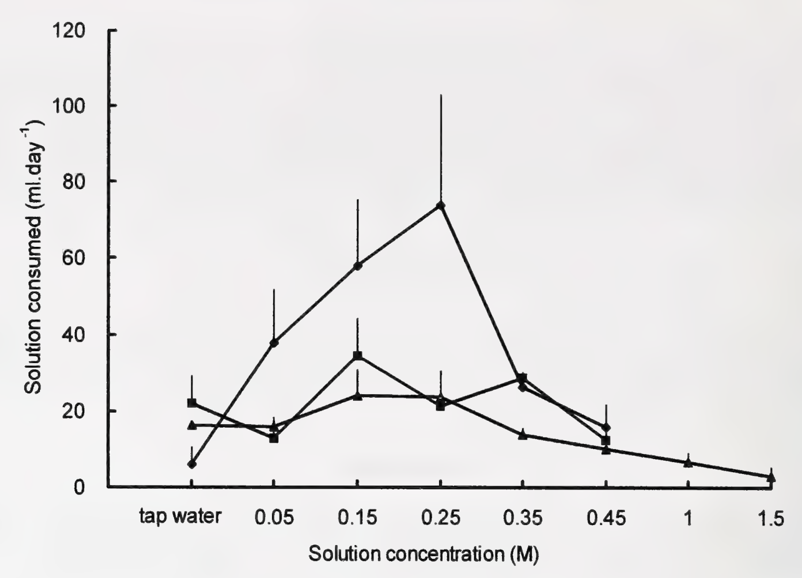


Fig. 1. Fluid consumption of *Akodon azarae* (■), *A. cursor* (◆), and *A. iniscatus* (▲) drinking various concentrations of sodium chloride solution. Vertical lines show +1SD.

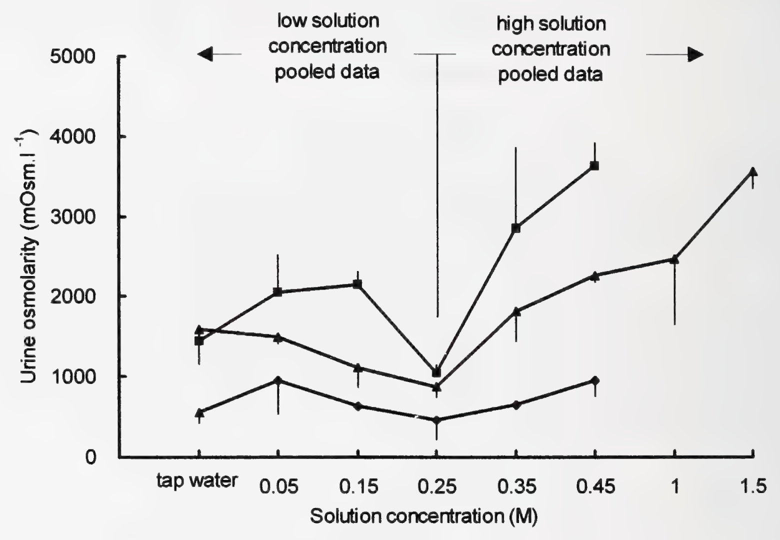


Fig. 2. Total urine concentration for *Akodon azarae* (■), *A. cursor* (◆), and *A. iniscatus* (▲) on fluid regime. Vertical lines show + or – 1SD.

than those observed for *A. cursor* (1 000 mOsmo, Tukey's test, $P < 0.05$). However, *A. iniscatus* reached this value at 1.5 M of ingested solution, whereas *A. azarae* and *A. cursor* reached it at a value of 0.45 M of ingested solution.

The intraspecific comparison of pooled data between low and high solution concentrations (Fig. 2) showed statistical differences in urine osmolarity for both *Akodon azarae* (t-test, n (low) = 12, n (high) = 8, $t = -4.2$, $df = 18$, $P < 0.001$) and *A. iniscatus* (t-test n (low) = 18, n (high) = 7, $t = -5.1$, $df = 23$, $P < 0.001$). On the other hand, these differences were not significant for *A. cursor* (t-test n (low) = 18, n (high) = 7, $t = -1.8$, $df = 23$, $P > 0.089$).

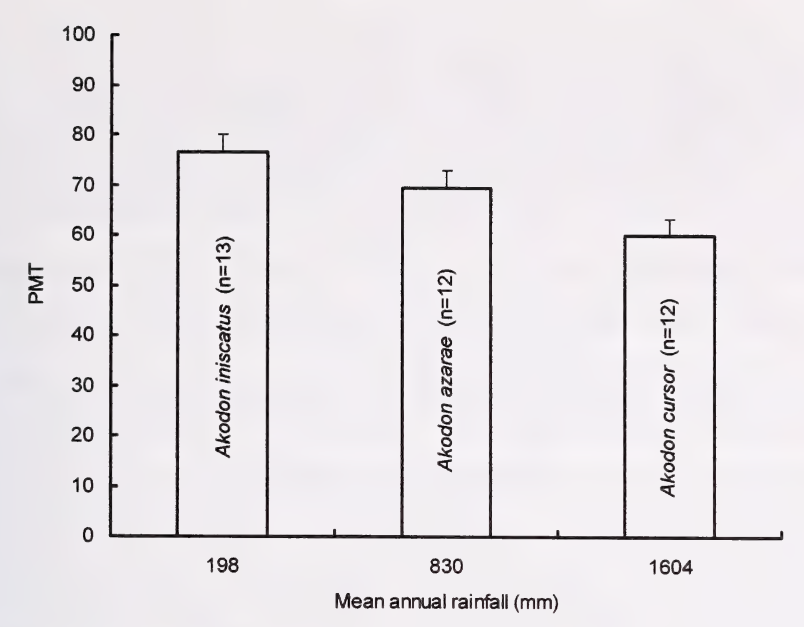


Fig. 3. Comparison of the percentage medullary thickness (PMT) of the kidneys of the selected *Akodon* species from three different rainfall regime areas. Vertical lines show + or – 1SD.

The interspecific comparison of pooled data at low and high solution concentration treatments showed that *Akodon azarae* exhibited the highest urine osmolarity followed by *A. iniscatus* and *A. cursor* (ANOVA, low: $F = 24.74$, $n = 46$, $df = 2$, $p < 0.001$; high: $F = 24.538$, $n = 26$, $df = 2$, $P < 0.03$).

Renal index (PMT)

The three species showed significant differences in percent of medullary thickness (PMT; ANOVA, $F = 71.87$, $n = 37$, $df = 2$; Tukey's test, $P < 0.001$). *Akodon iniscatus* showed the highest mean value (PMT = 76.5 ± 3.4 %, n = 13), *A. azarae* showed the medium mean value (PMT = 69.4 ± 3.6 %, n = 12) and *A. cursor* showed the lowest mean value (PMT = 60.1 ± 3.2 %, n = 12; Fig. 3).

Discussion

Small mammals vary dramatically in their ability to concentrate urine osmotically. Mesic mammals generally have a low capacity to concentrate urine and the rely on drinking as an avenue of water gain as was reported for many families of rodents (Whitford and Conley 1971; Greene and Fertig 1972; Mares 1977 a). On the other hand, small desert mammals cannot rely on drinking and their water requirements must be met by preformed water and/or metabolic water and by reducing the urinary water loss to a minimal level (Brooker and Withers 1994). These adaptations are well documented for *Dipodomys spectabilis* (Schmidt-Nielsen 1964) and *D. merriami* (Nagy and Gruchacz 1994).

Unlike the last rodent species cited above, the three species of *Akodon* studied presently, drink water to survive. However, at high concentrations of water solutions, these species do not drink and a progressive deterioration of body condition was observed.

With respect to urine concentration, urine osmolarity in species of *Akodon* differed after ingesting relatively low or high NaCl drinking solutions. Furthermore, there seems to be different renal handling of excess salt intake among the three species: *A. cursor*, which lives in higher rainfall areas, favor drinking relatively low concentrations of NaCl solution, and choose not to drink high NaCl solutions. In contrast, *A. iniscatus* and *A. azarae*, which live in dryer areas, did not drink substantial amounts of NaCl solutions, but showed good tolerance to high NaCl solutions, by forming a concentrated urine and conserving water.

Therefore, the general pattern of water-salt balance found in the three analysed species of *Akodon* was similar to that reported for *Rattus rattus*, *Phillotis osilae*, *Oryzomys longicaudatus*, *Akodon varius*, and some phillotine rodents (NORMAN and BAUDINETTE 1969; DUNSON and LAZELL 1982; MARES 1977 a; 1977 c).

Renal index has been regarded by some researchers as a good indicator of urine-concentrating ability in mammals (SCHMIDT-NIELSEN and O'DELL 1961). Significant relationships between urine concentrating ability, renal index, and the availability of water have been reported for the genera *Sylvilagus*, *Microtus*, and *Peromyscus* (HEISINGER and BREITENBACH 1969; HEISINGER et al. 1973, MACMILLEN 1983). On the other hand, BEUCHAT (1993) has found the renal index to be less reliable. BEUCHAT (1996) also found a significant relationship between the thickness of the inner medulla only in species from mesic environments, reflected in total medullary thickness, and the concentrating ability of the kidney. However, the percent of medullary thickness of the kidney (PMT) for *Akodon* species from xeric, mesic, and humid environments, was related to both the geographic rainfall regime and to its renal-concentrating ability.

Thus, intrageneric differences in urine concentrating capacity and renal morphology would be a consequence of the adaptive radiation of this genus in the earliest Pliocene (5.67 M. y. B. P. APFELBAUM and REIG 1989), related to different selection pressures.

Other influences such as diet, environmental conditions and behaviour affect the overall urine-concentrating ability (BEUCHAT 1990 a; 1990 b). Studies in natural conditions of these factors would be important to elucidate the physiological adaptations of these species.

Acknowledgements

The authors wish to express their gratitude to BOBY TAYLOR and Dra. GEORGINA BARRANTES for providing specimens of *Akodon iniscatus* and *Akodon cursor* used in this study. Thanks also to the late Dr. OSVALDO REIG and members of the Laboratorio de Histología for suggestions related to the planning of this work. We also thank Dr. OSCAR IRIBARNE, Dra. ALEJANDRA LOPEZ MAÑANES, Lic. ROXANA ZENUTO, Dra. ANA MALIZIA, and Dr. MARCELO KITTLEIN for improving the manuscript with their comments and suggestions. This work was granted by Universidad Nacional de Mar del Plata.

Zusammenfassung

Intragenerische Vergleiche zwischen der Fähigkeit, Urin zu konzentrieren und der Morphologie der Niere bei drei Akodon-Arten aus geographischen Regionen mit unterschiedlichen Niederschlagsmustern

Die Fähigkeiten zur Konzentration des Urins und die Morphologie der Nieren von *Akodon azarae*, *A. iniscatus* und *A. cursor* aus Regionen mit unterschiedlichen Niederschlagsmustern wurden untersucht. Im Gegensatz zu *A. iniscatus* verweigerten *A. azarae* und *A. cursor* NaCl-Lösungen über 0,45 M. *A. azarae* und *A. insicatus* können ihren Urin bis zu etwa gleichhohen Werten konzentrieren. Diese Werte lagen höher als bei *A. cursor*. Die Prozentwerte der Nierenmarklänge zeigen eine Beziehung zwischen dem Niederschlagsmuster der Region und der Urinmolarität.

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Z. Säugetierkunde **64** (1999) 285–297
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Genetic and morphological variation among populations of the bank vole *Clethrionomys glareolus* from north-eastern Poland: the seasonal aspect

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Reicept of Ms. 10. 03. 1999
Acceptance of Ms. 11. 05. 1999

Abstract

The relationship between genetic and morphological variation was studied in five populations of the bank vole (*Clethrionomys glareolus*) from NE Poland. For the assessment of genetic polymorphism 37 enzyme loci were investigated. The proportion of polymorphic loci (P) ranged from 0.162 to 0.270 and the average observed heterozygosity (H_0) from 0.074 to 0.095 in populations studied. F-statistics indicated the existence of seasonal variation in allele frequency in four populations ($F_{ST} = 0.011$–0.018, $p < 0.05$). The differentiation among vole populations was greater in autumn ($F_{ST} = 0.032$, $p < 0.0001$) than in spring ($F_{ST} = 0.023$, $p < 0.0001$). Morphometric variation in 3 groups of parameters (I – body size, II – size of internal organs, III – cranial and mandibular traits) was subjected to principal component analysis (PCA). There was a very clear separation of season in all three groups of parameters in each population. PCA analysis revealed differences among vole populations in body size, organ size and cranium size and shape in spring and only in body size and cranium shape in autumn. No correlation was found between Rogers' genetic distances and Mahalanobis distances, as calculated from 3 groups of morphological characters in both seasons ($r = |0.01–0.43|$, NS; Mantel's test). The data suggest that there is no equivalent degree of divergence on these two levels of integration in *C. glareolus*.

Key words: *Clethrionomys glareolus*, allozymes, morphometry, differentiation

Introduction

There is abundant geographic variation in both morphology and gene frequency in most species. The extent of geographic variation results from balance of forces tending to produce local genetic differentiation and forces tending to produce genetic homogeneity (SLATKIN 1987). Protein electrophoresis has been widely used to describe genetic differences among populations of rodent species (LEITNER and HARTL 1988; GALLARDO et al. 1992; GĘBCZYŃSKI et al. 1993; FEDOROV et al. 1995). The degree of genetic differentiation among populations over wide geographical distances is higher than within a narrow geographic area (GĘBCZYŃSKI et al. 1993; FEDOROV et al. 1995). It has also become obvious that there was considerable morphological variation among local populations of the species. Morphological differences between animals from various regions have hitherto mainly been related to the environmental conditions or, as in genetic instances, to the geographic distance and isolation (HAITLINGER 1965, 1970; HANSSON 1985; BAKER 1992; SARA and CASAMENTO 1995).

0044-3468/99/64/05 – 285 $ 12.00/0

Genetic and morphological observations are very rarely carried out on the same material. Thus, there were only a few estimations of the relationships between genetic and morphometric divergence among populations in mammals (HARTL et al. 1993; KITCHENER et al. 1994). On the other hand, there are numerous studies dealing with this problem in other groups of animals (LAZARIDOU-DIMITRIADOU et al. 1994; KYRIAKOPOULOU-SKLAVONOU et al. 1991; BAKER 1992; LOBO 1995).

The intrapopulation variability may have an effect on differences among populations. There is considerable evidence that body mass, organ weights, and gut morphology of rodents can change seasonally in response to changes in feeding habits, reproductive state, ambient temperature or photoperiod (HAMMOND 1993; NAGY and NEGUS 1993; HAMMOND and DIAMOND 1994; BORKOWSKA 1995; CAMPBELL and MACARTHUR 1996). Likewise, a spring generation of rodents differs in allele frequency from an autumn generation (FEDYK and GĘBCZYŃSKI 1980). Thus, seasonal variation may also be reflected in morphological and genetic differentiation among bank vole populations.

The bank vole, *Clethrionomys glareolus* (Schreber, 1780) is one of the most common Palearctic rodent species. It has a wide geographical distribution from the British Isles to Lake Baikal, and from Kola Peninsula to Asia Minor (RACZYŃSKI 1983). The genetic differences among bank vole populations have been determined in Austria (LEITNER and HARTL 1988) and Poland (GĘBCZYŃSKI et al. 1993). Morphological differences were found between eastern and western (HAITLINGER 1965) as well as between mountain and lowland vole populations in Poland (HAITLINGER 1970).

The purpose of this study was to determine variability in allozymes and morphology (body size, size of internal organs, and skull dimension) among the bank vole populations over short geographic distances. Next, the seasonal aspects of the interpopulation divergence will be taken into account.

Material and methods

A total of 391 individuals of *C. glareolus* was collected from 5 populations in the vicinity of Bialystok (NE Poland 23°07′E, 53°18′N, Tab. 1). The minimum distance between two sites was 10 km, maximum 50 km. Animals were caught in live-traps during two seasons: spring (May–June) and autumn (October–November) in 1995–97. The voles were brought into the laboratory and dissected. A spring generation of the bank vole consisted of over-wintered individuals, while in autumn the populations were only made up of current-year animals.

Samples of blood plasma, kidney, liver, and salivary gland were taken from each vole and stored at –85 °C until used for electrophoresis. Tissues were homogenized in phosphate buffer (0.01 M, pH 7.5) and then centrifuged at 12 000 rpm for 15 min at 4 °C. Protein electrophoresis was performed on (1) starch gel following the running and staining conditions given by SELANDER et al. (1971), HARRIS and HOPKINSON (1976), QUAVI and KIT (1980), and (2) cellulose acetate plates (SEARLE 1985), and (3) agar gel (NIELSEN 1977). Gene products for the following 37 presumptive enzyme loci were analysed. Locus were the following (E. C. number are given in parentheses): αGpd-1, αGpd-2, βGpd-1, and βGpd-2 (1.1.1.8), Sdh (1.1.1.14), Ldh-1 and Ldh-2 (1.1.1.23), Mdh-1 and Mdh-2 (1.1.1.37), Me-1 and Me-2 (1.1.1.40), Idh-1 and Idh-2 (1.1.1.42), Pgd (1.1.1.44), Dia (1.6.2.2), Cat (1.11.1.6), Sod-1 and Sod-2 (1.15.1.1), Aat-1 and Aat-2 (2.6.1.1), Pgm-1, Pgm-2, and Pgm-3 (2.7.5.1), EstB3 and EstD (3.1.1.1), Amy1-2 (3.2.1.1), Pep-2 and Pep-3 (3.4.11), Acy (3.5.1.14), Ald-1 and Ald-2 (4.1.2.13), Acon-1 and Acon-2 (4.2.1.3), Mpi (5.3.1.8), Pgi (5.3.1.9), Alb, and Prot. A locus was considered polymorphic if the frequency of the most common allele did not exceed 0.95. Alleles at polymorphic loci were designated alphabetically with increasing anodal migration of the corresponding allozymes.

BIOSYS-1 (SWOFFORD and SELANDER 1989) was used to calculate observed average heterozygosity (H_0) and χ^2 contingency test for homogenity. If significant deviation from Hardy-Weinberg equilibrium was found the fixation index F_{IS} was calculated. The deviation of F_{IS} from zero was tested by $\chi^2 = NF_{IS}^2$, where N is the total sample size (NEI 1977). Wright's F_{ST} was calculated to quantify the

amount of genetic differentiation between seasons in each population and among populations in spring and autumn, separately. An F-statistic value was considered to be significantly different from zero if statistically significant heterogeneity among samples at the same hierarchical level was found (χ^2 test). Pairwise Rogers' genetic distances (D_R) were estimated from allozyme data and clustered using the UPGMA method (Swofford and Selander 1989).

Morphometric variation in the 5 populations of the bank vole was assessed by taking 39 measurements on 349 individuals older than 3 months (age was determined according to Pucek and Zejda 1968). Morphological characters were divided into three groups:

I – body size (5 external measurements: total body mass TBM to the nearest 0.1 g, and head and body length HBL, tail length TL, hind foot length HFL, ear height EH to the nearest 0.01 mm; Pucek 1981);

II – organ size (13 internal measurements: dry mass of stomach STM, small intestine SIM, large intestine LIM, caecum CM, liver LM, kidneys KM, spleen SM, heart HM, lungs LUM, scraped mucosa SMM to the nearest 0.001 g, and length of small intestine SIL, large intestine LIL, and caecum CL to the nearest 0.01 cm; Myrcha 1964; Diamond and Karasov 1984; Hammond and Diamond 1994);

III – skull dimension (21 cranial measurements: condylobasal length CBL, total cranium length TCL, basal length BL, rostral width RW, interorbital width IW, zygomatic width ZW, mastoid width MW, palatal height PH, skull height per auditory bullae SPB, skull height between auditory bullae SBB, upper diastema length UDL, mandibule length ML, mandibular ramus height MH, recorded by dial caliper to the nearest 0.01 mm, and length of nasal bones NBL, length of frontal bones FBL, length of sagital crest SCL, length of interparietal bone IBL, incisive foramen length IFL, palatal length PL, upper molar series length from the alveoles UMSL, lower molar series length from the alveoles LMSL, recorded by binocular microscope with micrometer ocular to the nearest 0.01 mm; Haitlinger 1965; Viro and Niethammer 1982).

Morphological data were quantitatively compared in three groups separately by the use of principal component analysis (PCA, STATISTICA, StatSoft. Inc. 1995). The scores of the first principal component were used to calculate Mahalanobis distance (D^2) in a pairwise fashion between all populations in both seasons. To test differences among populations studied and seasons, ANOVA test and Fisher's least significant difference tests (L.S.D.) were performed on the first three factors of PCA (PC1, PC2, PC3). Mantel's (1967) test was used to test relationships between Rogers' genetic distances and Mahalanobis morphological distances among vole populations in both seasons. The analysis was performed using the TFPGA computer programme (Miller 1997).

Results

Genetic analysis

Fourteen of the 37 loci examined were found to be polymorphic in the bank vole from NE Poland, as defined using the 0.95 common allele frequency: Ldh-2, Me-2, Dia, Cat, Aat-2, Pgm-1, Pgm-2, Pgm-3, EstB3, EstD, Amyl-2, Pep-2, Acy, Mpi. But only five loci: Me-2, Dia, Pgm-3, EstB3, and Amyl-2 were polymorphic in every population studied and in both seasons. The percentage of polymorphic loci (P) ranged from 0.162 to 0.270 and the mean observed heterozygosity (H_0) from 0.070 to 0.095 in the bank vole populations (Tab. 1). There were no significant differences in observed heterozygosity H_0 between seasons in each population and among populations either in spring or in autumn ($p > 0.05$; Kruskal-Wallis test). Two populations in spring (BIA, ZED) and two others in autumn (PRZ, SZE) showed significant departures from Hardy-Weinberg equilibrium in a few loci (Tab. 2). There was a significant deficit of heterozygotes in all these populations.

To measure genetic differences between spring and autumn generations F_{ST} values were calculated (Tab. 3). In four populations mean F_{ST} values were statistically significant indicating that above 1 per cent of genetic variation in a *C. glareolus* population was attributable to differences between seasons. There was a low but significant genetic differen-

Table 1. Sample size (N), percentage of polymorphic loci (P) and observed heterozygosity (H_0) in spring and autumn generations of *C. glareolus*. Abbreviations of the populations are in parentheses.

Population		Spring generation			Autumn generation		
		N	P	H_0	N	P	H_0
Bialystok	(BIA)	44	0.216	0.074	71	0.243	0.075
Suprasl	(SUP)	31	0.216	0.081	38	0.270	0.079
Przewalanka	(PRZ)	31	0.243	0.094	41	0.270	0.079
Zednia	(ZED)	26	0.162	0.079	39	0.162	0.070
Szelagowka	(SZE)	29	0.216	0.081	41	0.243	0.086

Table 2. Allele frequencies at 14 polymorphic loci in spring (SG) and autumn (AG) generations of *Clethrionomys glareolus* from NE Poland. Asterisks indicated deviation from Hardy-Weinberg equilibrium.

Locus Allele	Bialystok		Suprasl		Przewalanka		Zednia		Szelagowka	
	SG	AG	SG	AG	SG	AG	SG	AG	SG	AG
Ldh-2										
a	0.977	0.965	1.000	1.000	0.968	1.000	0.981	1.000	0.983	0.902
b	0.023	0.035	0.000	0.000	0.032	0.000	0.019	0.000	0.017	0.098
Me-2										
a	0.798*	0.887	0.900	0.776	0.758	0.902	0.788	0.859	0.862	0.854
b	0.202*	0.113	0.100	0.224	0.226	0.037	0.212	0.141	0.138	0.146
c	0.000	0.000	0.000	0.000	0.016	0.061	0.000	0.000	0.000	0.000
Dia										
a	0.000	0.007	0.016	0.000	0.000	0.000	0.000	0.000	0.017	0.000
b	0.580	0.579	0.339	0.289	0.549	0.512	0.365*	0.423	0.414	0.512
c	0.420	0.414	0.645	0.711	0.419	0.450	0.635*	0.577	0.569	0.488
d	0.000	0.000	0.000	0.000	0.032	0.038	0.000	0.000	0.000	0.000
Cat										
a	0.000	0.007	0.017	0.053	0.000	0.000	0.000	0.038	0.000	0.000
b	1.000	0.993	0.983	0.947	1.000	1.000	1.000	0.962	1.000	1.000
Aat-2										
a	0.045*	0.021	0.017	0.053	0.000	0.000	0.000	0.000	0.000	0.000
b	0.955*	0.979	0.983	0.947	1.000	1.000	1.000	1.000	1.000	1.000
Pgm-1										
a	1.000	1.000	1.000	0.987	0.855	0.902	1.000	1.000	0.948	0.976
b	0.000	0.000	0.000	0.013	0.145	0.098	0.000	0.000	0.052	0.024
Pgm-2										
a	0.000	0.014	0.033	0.053	0.081	0.061	0.000	0.000	0.017	0.012
b	0.886	0.928	0.919	0.868	0.919	0.939	0.962	0.987	0.862	0.854
c	0.014	0.058	0.048	0.079	0.000	0.000	0.038	0.013	0.121	0.134
Pgm-3										
a	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000
b	0.083	0.164	0.167	0.171	0.081	0.134*	0.135	0.244	0.225	0.390
c	0.119	0.236	0.233	0.092	0.339	0.232*	0.327	0.192	0.155	0.146
d	0.298	0.257	0.150	0.184	0.177	0.146*	0.173	0.128	0.241	0.184
e	0.500	0.336	0.433	0.553	0.403	0.488*	0.365	0.436	0.379	0.280
f	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 2. (Continued)

Locus Allele	Bialystok		Suprasl		Przewalanka		Zednia		Szelagowka	
	SG	AG	SG	AG	SG	AG	SG	AG	SG	AG
EstB3										
a	0.761	0.791	0.600	0.750	0.694	0.720	0.673	0.718	0.690	0.598
b	0.239	0.209	0.317	0.237	0.306	0.280	0.308	0.282	0.293	0.378
c	0.000	0.000	0.083	0.013	0.000	0.000	0.019	0.000	0.017	0.024
EstD										
a	0.875	0.887	0.862	0.921	0.806	0.793	0.808*	0.962	0.948	0.878
b	0.125	0.113	0.138	0.079	0.194	0.171	0.192*	0.038	0.052	0.122
c	0.000	0.000	0.000	0.000	0.000	0.037	0.000	0.000	0.000	0.000
Amy1-2										
a	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000
b	0.667*	0.843	0.750	0.908	0.733	0.859	0.812	0.784	0.727	0.868*
c	0.333*	0.157	0.229	0.092	0.267	0.141	0.188	0.216	0.273	0.132*
Pep-2										
a	0.102	0.086	0.065	0.013	0.016	0.063	0.000	0.000	0.071	0.159*
b	0.898	0.900	0.935	0.974	0.984	0.913	0.981	1.000	0.875	0.817*
c	0.000	0.014	0.000	0.013	0.000	0.024	0.019	0.000	0.054	0.024*
Acy										
a	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000
b	0.045	0.028	0.000	0.158	0.000	0.037	0.000	0.077	0.000	0.012
c	0.955	0.972	0.967	0.842	1.000	0.963	1.000	0.923	1.000	0.988
Mpi										
a	0.000	0.000	0.000	0.000	0.016	0.013	0.000	0.000	0.000	0.000
b	0.000	0.000	0.000	0.000	0.065	0.074	0.019	0.000	0.034	0.000
c	0.989	0.936	0.968	0.971	0.903	0.913	0.981	1.000	0.949	1.000
d	0.011	0.064	0.032	0.029	0.016	0.000	0.000	0.000	0.017	0.000

Table 3. Mean F-statistic values at all loci for seasonal generations in five populations of *Clethrionomys glareolus* from NE Poland. Asterisks denote statistical significance for F_{ST} as determined by the χ^2 test (see text); *p < 0.05; **p < 0.01; NS = nonsignificant. Site abbreviations as in Tab. 1.

Population	F_{IS}	F_{IT}	F_{ST}
BIA	0.089	0.100	0.012**
SUP	0.004	0.022	0.018**
PRZ	0.033	0.043	0.011*
ZED	0.007	0.018	0.011*
SZE	–0.048	–0.036	0.012 NS

tiation among the bank vole populations in spring (mean $F_{ST} = 0.023$; $p < 0.0001$) in eight loci (Dia, Aat-1, Pgm-1, Pgm-2, Pgm-3, EstB3, Pep-2, Acy). However, in autumn the mean F_{ST} value was higher ($F_{ST} = 0.032$; $p < 0.0001$) and 16 single locus F_{ST} values were statistically significant (Ldh-1, Ldh-2, Me-2, Idh-1, Pgd, Dia, Cat, Aat-1, Aat-2, Pgm-1, Pgm-2, Pgm-3, EstD, Pep-2, Acy, Mpi). Rogers' genetic distance estimates based on pairwise comparisons of the five sites ranged from 0.018 to 0.029 in spring and from 0.023 to 0.039 in autumn, indicating that populations were very similar to one another. The linkage distances were so low that any groupings in the clusters could be considered to be random associations. However, two geographical nearest populations (SUP and ZED)

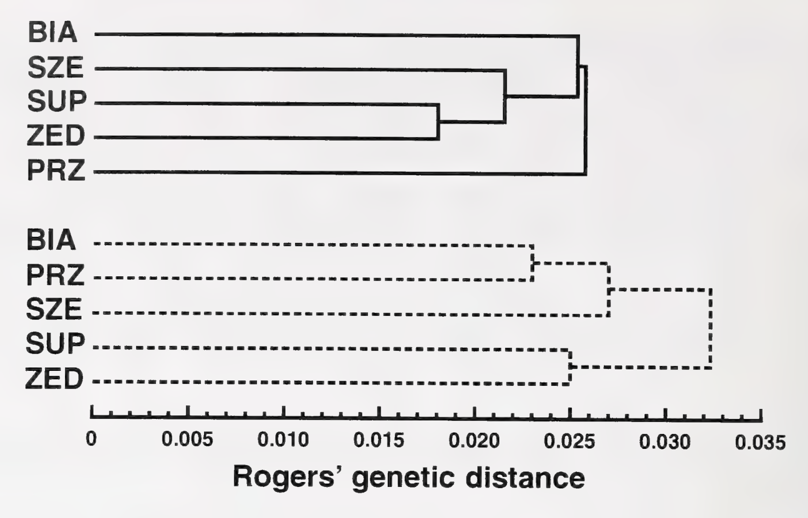


Fig. 1. Phenogram generated by UPGMA cluster analysis based on Rogers' genetic distances among five populations of *C. glareolus* in spring (solid lines) and autumn (broken lines). Site abbreviations as in Tab. 1.

clustered together in both seasons (Fig. 1). Correlation of two genetic distance matrices from various seasons revealed that genetic differentiation among the bank vole populations in spring was not covered by interpopulation differentiation in autumn ($r = 0.06$, $Z = 0.01$; NS; Mantel's test).

Morphological variation

Seasonal variation was conspicuous in all the populations studied. The first principal component (PC1) explained over 50% of the total variation in body size (I) and about 40% in organ size (II) and cranium dimension (III) in each population. Nevertheless, the between-season variation in three groups of morphological parameters described by PC1 was significant in all populations of the bank vole (Tab. 4).

Principal component analyses of *C. glareolus* revealed significant differences in body size (group I) among populations both in spring (ANOVA on PC1: $F = 7.24$; $p < 0.0001$) and autumn (ANOVA on PC1: $F = 10.12$; $p < 0.0001$). However, the first PC based on group II of morphological parameters divided the bank vole populations only in spring ($F = 2.78$; $p < 0.05$) but not in autumn ($F = 1.01$; NS). The first component (PC1) based on craniometric data (group III) explained 36% of total amount of phenotypic variability in spring and about 32% in autumn (Tab. 5). The differences observed among the bank vole populations also referred to skull dimension. The PC1s were of the size-type with all coefficients positive in both seasons, which suggested an influence of overall skull size on group separation. The second factor (PC2) based on craniometric parameters accounted for 8.8% of the variation in spring. In this season it loaded positively on measurements of skull and mandibule length (CBL, TCL, BL, UDL, ML) and negatively on parameters of skull width (RW, IW, ZW) and height (PH, SPB, SBB; Tab. 5). Thus, PC2 could be interpreted as a shape-type component in spring. In autumn, however, the second (PC2) and the third (PC3) factors which explained 24.3% of the total variance together represented 'shape' variation (Tab. 5). Analyses of variance confirmed that in spring the bank vole populations differed significantly in cranium size (PC1: $F = 6.45$; $p < 0.0001$) and cranium shape also (PC2: $F = 4.18$; $p < 0.01$, PC3: $F = 13.59$; $p < 0.0001$).

Table 4. Seasonal variation in body size (I), organ size (II), and skull dimension (III) in five populations of Clethrionomys glareolus from NE Poland revealed by one-way ANOVA on PC1. EV = eigenvalue, V = per cent of total variance, p = significance level for between-season comparison in ANOVA. Only factor loading values greater than absolute 0.60 are presented. Site abbreviations as in Tab. 1. Acronyms are described in the text.

Population		EV	V	Factor loadings	p
BIA	I	2.67	53.44	HBL (0.91), TBM (0.85), TL (0.74)	0.0000
	II	4.61	35.43	LM (0.84), KM (0.78), SIM (0.77), SMM (0.70)	0.0000
	III	6.56	31.23	BL (–0.96), CBL (–0.95), TCL (–0.92), UDL (–0.81), ZW (–0.78), MW (–0.76)	0.0003
SUP	I	3.18	63.68	HBL (0.92), TBM (0.88), TL (0.82)	0.0000
	II	6.68	51.42	STM (0.91), KM (0.87), LIM (0.83), SIM (0.82), HM (0.80), CM (0.78), LUM (0.74)	0.0000
	III	8.45	40.26	TCL (0.97), CBL (0.95), BL (0.94), NBL (0.85), ZW (0.83), ML (0.83), UDL (0.82), IFL (0.72)	0.0009
PRZ	I	3.13	62.66	TBM (–0.94), HFL (–0.92), EH (–0.82), TL(–0.77)	0.0000
	II	5.89	45.29	SIM (0.89), STM (0.83), SMM (0.82), LUM (0.82), CM (0.80), LIM (0.75)	0.0000
	III	6.99	33.30	CBL (0.88), BL (0.86), MW (0.77), ZW (0.73), FBL (0.72), UDL (0.71)	0.0000
ZED	I	2.76	55.22	TBM (–0.93), HBL (–0.93), TL (–0.84)	0.0000
	II	6.11	47.01	STM (0.91), CM (0.84), KM (0.83), SIM (0.82), LIL (0.70)	0.0000
	III	9.04	43.07	TCL (–0.94), CBL (–0.93), BL (–0.93), ZW (–0.84), NBL (–0.84), MW (–0.80), UDL (–0.77), FBL (–0.76), IFL (–0.74)	0.0000
SZE	I	3.24	64.84	HBL (0.93), TBM (0.85), EH (0.84), TL (0.78)	0.0000
	II	4.59	35.30	STM (0.90), CM (0.85), KM (0.82), HM (0.75)	0.0000
	III	7.93	37.78	BL (0.93), CBL (0.92), TCL (0.92), UDL (0.88), ML (0.88), ZW (0.80), NBL (0.80), MW (0.72), IFL (0.71)	0.0106

However, two 'shape' components (PC 2 and PC 3) only separated vole populations in autumn (ANOVA on PC 1: $F = 1.46$; NS, PC 2: $F = 19.71$; $p < 0.001$, PC 3: $F = 11.76$; $p < 0.0001$).

Mahalanobis distances (D^2) calculated from the first principal component based on group I of morphological parameters ranged from 0.046 to 1.456 among populations in spring and from 0.001 to 1.618 in autumn. The differences in organ and cranium size (PC 1 based on group II and III) were not found among populations in autumn. Thus, in this season the Mahalanobis distances among populations based on these two groups of variables ranged only from 0.0–0.587. Likewise, D^2 index also reached the low values when we analysed differences among populations in size of voles internal organs (group II; D^2 range 0.023–0.426) and cranium size (group III, D^2 range 0.022–1.317) in spring. Cluster diagrams generated on the basis of Mahalanobis distances from group I of morphological parameters were similar in spring and autumn ($r = 0.71$; Mantel's test) but the correlation coefficient was not significant ($Z = 2.16$; $P = 0.0560$, Fig. 2 A). There was no significant correlation in Mantel's test between matrices of Mahalanobis distances in spring and autumn based on group II ($r = -0.34$, $Z = 0.10$; NS, Fig. 2 B) and group III of morphological parameters ($r = -0.28$, $Z = 0.75$; NS, Fig. 2 C).

Table 5. Component loadings for the first three principal components (PC1, PC2, PC3) analysed in spring and autumn generations of *Clethrionomys glareolus*. Five populations are included in the analysis and PCA is based on 21 craniometric variables. EV = eigenvalue, V = per cent of total variance. Acronyms are described in the text.

Variables	Spring generations			Autumn generation		
	PC1	PC2	PC3	PC1	PC2	PC3
CBL	0.900	0.245	–0.001	0.914	0.164	–0.086
TCL	0.890	0.137	–0.026	0.893	0.200	–0.028
BL	0.916	0.217	–0.058	0.885	0.151	–0.129
RW	0.486	–0.018	0.156	0.570	0.101	0.080
IW	0.501	–0.250	0.206	0.189	0.273	–0.185
ZW	0.752	–0.117	0.057	0.647	0.419	–0.248
MW	0.739	–0.279	0.115	0.711	0.316	–0.216
PH	0.461	–0.178	–0.076	0.437	–0.516	0.351
SPB	0.554	–0.595	0.259	0.421	0.090	0.414
SBB	0.451	–0.688	0.211	0.297	0.014	0.556
UDL	0.722	0.346	0.313	0.777	0.090	0.026
ML	0.804	0.092	–0.049	0.709	0.108	–0.048
MH	0.450	–0.099	–0.254	0.424	0.406	–0.362
NBL	0.647	0.264	–0.106	0.708	–0.275	–0.187
FBL	0.658	–0.041	0.184	0.404	–0.705	–0.136
SCL	0.149	–0.023	–0.060	0.043	0.605	0.358
IBL	0.004	–0.060	0.030	0.269	–0.073	0.524
IFL	0.570	0.479	–0.094	0.502	–0.587	–0.060
PL	0.225	0.348	–0.191	0.205	–0.071	0.546
UMSL	0.230	–0.294	–0.799	0.313	–0.671	–0.167
LMSL	0.375	–0.249	–0.718	0.261	–0.808	–0.256
EV	7.58	1.85	1.62	6.64	3.31	1.74
V	36.09	8.82	7.71	31.63	15.75	8.40

Table 6. Correlation between Rogers' genetic distances D_R and Mahalanobis distances D^2 calculated from PC1 of groups I, II, and III of morphological parameters in spring (SG) and autumn (AG) generations of *Clethrionomys glareolus*. r = correlation coefficient, Z = statistic value, p = probability level after randomly permuting the values in one of the distance matrices 1 000 times, Mantel test.

Comparison	Generation	r	Z	p
$D_R \times D^2$ (I)	SG	0.07	0.10	NS
	AG	–0.38	0.16	NS
$D_R \times D^2$ (II)	SG	0.43	0.04	NS
	AG	0.01	0.02	NS
$D_R \times D^2$ (III)	SG	0.17	0.10	NS
	AG	0.23	0.05	NS

Correlation between genetic and morphological divergence

Cluster diagrams generated on the basis of Rogers' distances and Mahalanobis distances (in three groups of parameters separately) were not similar either in spring or in autumn, suggesting no equivalent degree of divergence on the two levels of integration. To quantify the lack of this relationship correlation coeffcients between D_R matrices and D^2 matrices were calculated, with regard to season and group of morphological parameters (Tab. 6). The correlation coefficients (r) were low and not significant in all cases of Mantel's test.

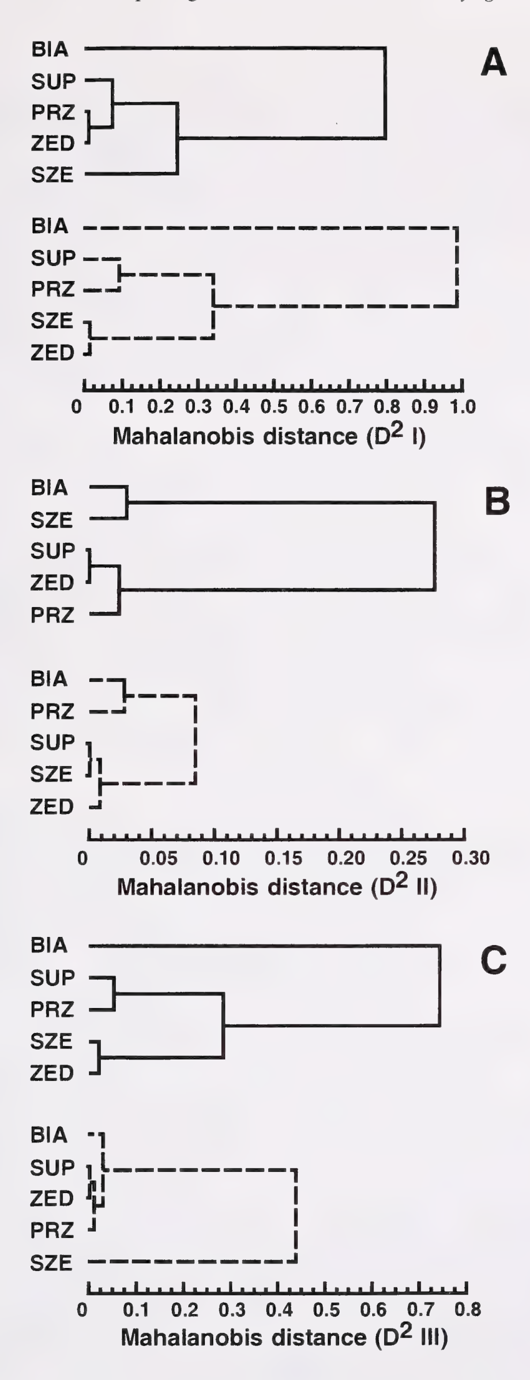


Fig. 2. UPGMA cluster analysis using Mahalanobis distances based on PC1 from morphological data of (a) group I (D^2I), (b) group II (D^2II) and (c) group III (D^2III) among *C. glareolus* populations in spring (solid lines) and autumn (broken lines). Site abbreviations as in Tab. 1.

Discussion

There are three general areas where the present data are noteworthy. Firstly, the bank vole populations differed from each other over short geographical distances both genetically and morphologically. Secondly, the genetic and morphological divergence among populations varied between seasons. Finally, there was no correlation between genetic and morphological differentiation of the populations in both seasons.

The results of the analyses on allozyme variation in *C. glareolus* indicated that genetic polymorphism is not relatively high in this species. Percent of polymorphic loci in the populations studied approximated the values obtained for other populations of the bank vole in Poland (Fedyk and Gębczyński 1980; Gębczyński et al. 1993; Gębczyński and Ratkiewicz 1998). However, the observed heterozygosity (H_0) slightly exceeded H_0 values obtained both in Poland ($H_0 = 0.073$; Gębczyński and Ratkiewicz 1998) and in Austria ($H_0 = 0.075$; Leitner and Hartl 1988).

Morphological analysis supported that the bank vole populations exhibited body size, organ, and cranium size variation within its distribution, even over short geographical distances. It is known that *C. glareolus* from various geographical regions differs considerably in intestinal morphology and body size (Hansson 1985). Comparison of Western and Eastern Polish bank voles revealed the presence of several skull characters differing among the populations (Haitlinger 1965). Likewise, mountain populations of *C. glareolus* differed from lowland populations in respect to dimensions and proportions of the body and skull (Haitlinger 1970). According to Hansson (1985), all geographical differences in *C. glareolus* are related to ecogeographical rules, to possible demographic patterns, and to various adaptations following different modes of feeding (i. e., more granivores or more foliovores animals). However, morphological differences observed among the bank vole populations over short geographical distances seem to be due to adaptations to various local habitats.

Genetic structure of the population changes between seasons in four out of five bank vole populations. Differences in allele frequency between spring and autumn generations of *C. glareolus* have been already noted (Fedyk and Gębczyński 1980; Gębczyński and Ratkiewicz 1998). It is interesting that seasonal intrapopulation variability strongly affected divergence among vole populations. Thus, the differentiation among autumn populations was greater than among those in spring. Furthermore, correlation of two genetic distance matrices from spring and autumn revealed that genetic differentiation among the bank vole populations was not equivalent in various seasons. Smaller differences among vole populations in spring than in autumn suggested elimination of rare heterozygotes from the populations. Winter mortality can reach 77% of autumn numbers in *C. glareolus* (Pucek et al. 1993). However, it did not cause between-season changes in H_0 value, as Gębczyński and Ratkiewicz (1998) noted, but decreased the F_{ST} value, the measure of genetic differences among populations. Next, throughout breeding season the intrapopulation genetic variability increased. It seems that two processes, dispersion and mating system, can be responsible for increasing the intrapopulation variability, and consequently increasing F_{ST} value among populations in autumn. The dispersal rates of *C. glareolus* individuals vary significantly with seasons, being the highest in early summer and in autumn (Gliwicz 1988). Additionally, *C. glareolus* was characterized by a promiscuous mating system, and multiple paternity was common in natural populations (Ratkiewicz and Borkowska 1999). Hence, there was a deficit of homozygotes at all loci, showing significant departures from Hardy-Weinberg equilibrium.

Seasonal variation in morphological parameters of the bank vole occurred in each population studied. The dynamic aspect of body mass and gut size of small herbivores was widely noted and explained as a physiological response to fluctuating environmental conditions (Hammond 1993; Borkowska 1995; Campbell and MacArthur 1996). Con-

trary to the genetic data, the differentiation in body size among bank vole populations was similar in spring and autumn. Therefore, it seems that body size could be an indicator of morphological divergence among populations of the bank vole. However, variation in size of internal organs strongly depended on a state of sexual activity (Hammond and Diamond 1994) or food availability (Campbell and MacArthur 1996). This is why the differences in group II in morphological parameters appeared among populations only in spring. The divergence in cranium dimension demonstrated seasonal variation also. Thus, cranium size and shape divided the populations in spring. However, individual variation related to age in craniometric parameters (Haitlinger 1965) is high in autumn populations, which consisted of relatively young animals. Thus, the 'shape' components (PC2 and PC3) only separated vole populations in this season.

Genetic and morphological differentiation patterns were discordant in *C. glareolus*. The analyses revealed that in both seasons allozymic variation did not correspond to morphological variation specified either by body size, or by size of internal organs, or by cranium dimension. Among the studies that have combined electrophoretic and adequate morphometric data to examine intraspecific population differentiation patterns, discordant genetic and morphological differentiation was found in amphibians (Kyriakopoulou-Sklavounou et al. 1991) and birds (Baker 1992). The authors suggested that genetic patterns were haphazard, while the morphological differences were due to either climatic adaptation or random divergence through founder effects. On the other hand, changes in environmental conditions, either temporarily or permanently, strongly influence both genetic and morphological variance among populations of small mammals. Thus, it seems that a temporal variation in the genetic and morphological constitution of a population has the potential for revealing the agents responsible for microevolutionary change.

Acknowledgements

I would like to thank Prof. M. Gębczyński for his attention to this work and critical reading of the manuscript. I am also grateful to Dr. M. A. Ratkiewicz for his advice and help with electrophoresis.

Zusammenfassung

Genetische und morphologische Differenzierung zwischen Rötelmauspopulationen (Clethrionomys glareolus) aus dem Nordosten Polens: Saisonale Aspekte

Bei 5 Rötelmauspopulationen (*Clethrionomys glareolus*) aus dem Nordosten Polens wurde die genetische und morphologische Variabilität untersucht. Zur Abschätzung der genetischen Variabilität wurden 37 Enzymloci mittels Proteinelektrophorese untersucht. Der Polymorphiegrad (P) reichte von 0,162 bis 0,270 und der durchschnittliche beobachtete Heterozygotiegrad (H_0) von 0,047 bis 0,095. Berechnungen zur F-Statistik ergaben das Auftreten von saisonalen Unterschieden in den Allelfrequenzen von vier Populationen ($F_{ST} = 0{,}011–0{,}018$, $p < 0{,}05$). Die Differenzierung zwischen den Rötelmauspopulationen war im Herbst ($F_{ST} = 0{,}032$, $p < 0{,}0001$) größer als im Frühling ($F_{ST} = 0{,}023$, $p < 0{,}0001$). Die morphometrische Variation in drei Gruppen von Parametern (I – Körpergröße, II – Größe innerer Organe, III – Schädelmaße) wurde mittels Hauptkomponentenanalyse (PCA) untersucht. In allen drei Parametergruppen zeigten sich klare saisonale Unterschiede. Die PCA ergab Unterschiede zwischen den Rötelmauspopulationen hinsichtlich der Körpergröße, der Größe innerer Organe sowie der Schädelgröße und -form für den Frühling, während sie sich im Herbst nur in bezug auf die Körpergröße und die Schädelform unterschieden. Genetische Distanzen nach Rogers und Mahalanobis-Distanzen, berechnet für 3 Gruppen morphologischer Merkmale in beiden Jahreszeiten, waren nicht miteinander korreliert ($r = |0.01–0.043|$, NS; Mantel-Test). Nach unseren Daten zeigen bei der Rötelmaus die beiden untersuchten Merkmalssysteme keinen vergleichbaren Grad an Differenzierung zwischen Populationen.

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Z. Säugetierkunde **64** (1999) 298–307

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Reevaluation of the taxonomic status of North African gerbils usually referred to as *Gerbillus pyramidum* (Gerbillinae, Rodentia): Chromosomal and biometrical data

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Receipt of Ms. 14. 12. 1998
Acceptance of Ms. 05. 05. 1999

Abstract

The chromosomal and biometrical attributes of large-sized, hairy-footed gerbils from North Africa usually referred to as *Gerbillus pyramidum* were studied. High-resolution banding techniques as well as external and skull biometry were used to compare specimens from Mauritania and Algeria. All specimens studied were characterized by the same karyotype, comprising 40 chromosomes and 74 autosomal arms. Gerbils from Algeria were found to be larger than those from Mauritania for most of the skull measurements, as well as for some external measurements. Comparisons with published data from other North African countries (Senegal, Morocco, Tunisia) suggest that all the previously figured 2 n = 40 karyotypes do represent the same species, chromosomally significantly distinct from 2 n = 38 chromosome individuals found in Egypt and Sudan that correspond to true *Gerbillus pyramidum*. Based on our results and awaiting contrary evidence, we propose that the 2 n = 40 chromosome specimens found from Senegal to Libya correspond to a unique species, for which the name *Gerbillus tarabuli* should be applied. This species of wide distribution in northern Africa shows an apparently important biometrical variability, to be related with eco-climatological variations of the environment in which these populations live.

Key words: *Gerbillus*, North Africa, chromosomes, biometry, systematics

Introduction

Rodents of the genus *Gerbillus* constitute a significant part of the arid and semiarid communities of mammals, from North Africa to India through the Arabian Peninsula and the Middle East. From a taxonomic point of view, their diversity is established, but, as stated by Musser and Carleton (1993), ... "[t]his genus has never been adequately revised". As a result, the number of species recognized has varied considerably according to various authors (see review in Lay 1983), until Lay (1983) produced a list of 62 tentative species which was nearly entirely adopted by Musser and Carleton (1993). Clearly identified in these lists, a number of taxonomic questions remained. Part of this problem undoubtly lies in the great number of ancient, often superficial, descriptions of new taxa that were only based on crude comparisons of colour and other morphological (external and a few skull) characteristics. The use of new morphological characters (see Lay 1983) and, more importantly, the development of cytogenetical investigations (starting from Matthey 1952) have improved our knowledge of the systematics in this group, without providing, however, significant clarification in its taxonomic arrangement to date.

0044-3468/99/64/05 – 298 $ 12.00/0

Among the taxonomical problems identified in *Gerbillus*, the status of large-sized, hairy-footed gerbils from North Africa, the Sinai, and Israel that have been referred to as *Gerbillus pyramidum* Geoffroy, 1825 is still a matter of debate. Often considered to include populations of individuals characterized by diploid numbers of chromosomes (2 n) ranging from 38 (Wassif et al. 1969) to 66 (Wahrman and Zahavi 1955), the name *G. pyramidum* was restricted by Lay (1983, following Lay et al. 1975) to 2 n = 38 specimens from Egypt and Sudan. According to the latter author, the populations from the Sinai and coastal areas of Israel characterized by high diploid numbers should be referred to a species yet to be identified, but probably different from *G. pyramidum*. On the other hand, populations from North Africa west of Egypt and Sudan have been studied by various authors, under different species names. When performed, standard chromosomal analyses regularly yielded 2 n = 40 chromosomes for individuals from these populations: Tunisia (Jordan et al. 1974; Chibani and Lamine-Cheniti 1982), Morocco (Lay et al. 1975), Algeria (Matthey 1952), Mauritania (Klein et al. 1975), Senegal (Hubert and Böhme 1978; Granjon et al. 1992). In this region, two species have been described, which are proposed by Lay (1983) as potentially valid, and possibly characterized by this diploid number of 40 chromosomes. These are *G. tarabuli* described by Thomas (1902) from Libya (initially as a subspecies of *G. pyramidum*), and *G. riggenbachi*, described by the same author (Thomas 1903) from Western Sahara (and then said to be ... "[a] representative of *G. pyramidum*").

In this study, we investigate gerbils from Mauritania and Algeria using high resolution chromosome banding techniques, and also bring together all the available biometrical information (including original one) on these large-sized gerbils from North Africa, with the aim of discussing the systematic implications of these data, and making some suggestions about the nomenclature in this group.

Material and methods

The skulls and skins of the specimens studied are deposited in the collection of the Laboratoire de Zoologie, Mammifères et Oiseaux, at the Museum National d'Histoire Naturelle. The tissue explants and a portion of the cells of the karyotyped specimens are routinely kept in liquid nitrogen in the cell and tissue collection of the same laboratory.

Chromosomal analyses

Six specimens (3 females and 3 males) of large-sized, hairy-footed gerbils from coastal areas of Mauritania, as well as two specimens (one female and one male) from Béni Abbès (Algeria) have been karyotyped. Chromosome analysis was performed on preparations obtained from fibroblast cultures established after tail biopsy. Mitotic chromosomes were studied by G-banding (GTG; Seabright 1971), R-banding (RBG; Viegas-Pequignot and Dutrillaux 1978) and C-banding (CBG; Sumner 1972; see ISCN 1995). For each specimen, at least 20 metaphases were analysed. The origin, sex, and number of the specimens studied are as follows: Mauritania: from Ivik, Banc d'Arguin (male n° 88–006); near Nouamghar (female n° 95–002; male n° 95–007); surroundings of Nouakchott (male n° 95–035; female n° 95–081); Tamzakt (male n° 95–082). Algeria: from Béni-Abbès (male n° 97–013; female n° 97–044).

Morphometric analyses

Preliminary analyses have revealed the presence of at least 4 species of *Gerbillus* in coastal areas of Mauritania (Granjon et al. 1997). Among them, a sample of 27 adult specimens of large-sized, hairy-footed gerbils referable to the species with 2 n = 40 chromosomes has been isolated, on the basis of the confrontation of cytogenetical, morphological, and biometrical results (unpubl. data). The sample from Algeria is composed of 15 adult specimens from Béni Abbès and El Goléa. On all these specimens, classical external measurements (weight, head and body, tail, hind foot, and ear length) have been taken, as well as 8 skull measurements: GLS (greatest length of skull), ZYW (greatest zygomatic width), IOB (least

breadth of interorbital constriction), DIA (length of diastema), LPF (length of palatal foramina), UTR (crown length of upper tooth row), BBC (breadth of braincase) and BUL (greatest length of bullae). These measurements have been taken as described in Chimimba and Dippenaar (1995). They were selected for comparative purpose with other studies, being the more regularly presented measurements on *Gerbillus* skulls. The origin, sex, and number of the specimens studied are as follows: Mauritania: from the surroundings of Nouakchott, Trarza (females n° 1994.1273 and 1997.1495, male n° 1994.1272); from Nbeika, Tagant (male n° 1997.1479); from Agneitir, Inchiri (female n° 1997.1481); from Sei-Rakna, Trarza (females n° 1997.1484 and BLM386, male n° BLM388); from Amatlich El Gleitat, Adrar (male n° 1997.1480); from Tiguent, Trarza (female n° 1997.1486, males n° 1997.1485, and BLM391); from Tamzakt, Trarza (female n° 1997.1494, males n° 1997.1482, 1997.1483, 1997.1491, BLM448, and BLM455); from Chott Boul, Trarza (females n° 1997.1490, 1997.1496, 1997.1497, BLM441, and BLM459A, male n° 1997.1489); from Akchar, Inchiri (female n° 1997.1474, male n° BLM423); from Hassi Tifouggag, Brakna (male n° 1997.1493). Algeria: from El Goléa (females n° 1997.503, 1997.504, 1997.505, and 1997.506, males n° 1997.507 and 1997.508); from the surroundings of Beni-Abbès (males n° 1997.509, 1997.510, 1997.511, 1997.513, 1997.514, 1997.515, and 1997.516, females n° 1997.512 and 1997.517).

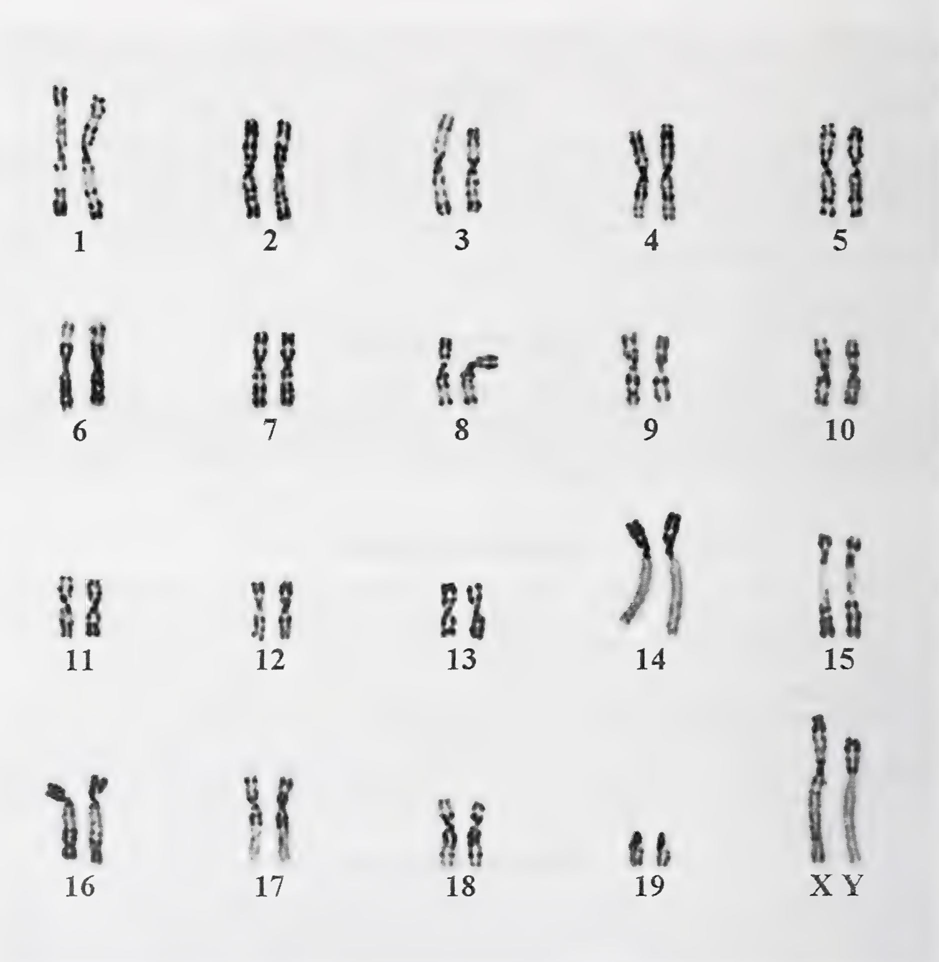


Fig. 1. R-banded (RBG) karyotype of a male *G. tarabuli*. Note that in addition to the late replicating long arm of the Y chromosome, the long arm of pair 14, an intercalar segment of the long arm of pair 1 and distal segments of the pairs 17 and 18 are also late replicating.

Results

Chromosomal analysis

After R-banding, the karyotypes of the six specimens from Mauritania and the two specimens from Algeria were found to be identical. They consist of 40 chromosomes comprising 13 pairs of metacentric, 5 pairs of submeta- to subtelocentric and one pair of acrocentric chromosomes, resulting in a number of autosomal arms (NFa) of 74. Both sex chromosomes are large submetacentrics, the X chromosome being the largest of the set and the Y chromosome being equal in size to the second pair of autosomes. Their short arms are identical and result from an autosome-gonosome translocation (Fig. 1). In spite of the important quantity of C heterochromatin revealed in all centromeric and some intercalar regions (Fig. 2), no well-defined heteromorphism for C-band positive heterochromatin was observed.



Fig. 2. C-banded (CBG) karyotype of male *G. tarabuli*. Note that the late replicating segments of the Fig. 1 are C-band positive.

Morphometric data

The ranges of variation of the measurements taken on the samples from Mauritania and Algeria are given in tables 1 (body measurements) and 2 (skull measurements), together with the values extracted from various other studies. No statistical test could be performed between our data and those from other authors, due to the fact that individual data (and/or standard deviation values) were rarely available in the latter. Between the series of Algeria and Mauritania that we measured, significant differences were found for all skull measurements, except diastema length (Mann-Whitney U tests, $p < 0.05$), the specimens from Algeria being consistently larger. As far as body measurements are concerned, Algerian specimens were found to be larger for hindfoot (U test, $p = 0.0003$) and weight (U test, $p = 0.014$) values, whereas Mauritanian specimens were found to be larger for tail length (U test, $p = 0.0001$) and ear length ($p = 0.0314$) values.

For Mauritania, our data mostly fall in the range of the values given by KLEIN et al. (1975) for a sample of *Gerbillus* sp. "*agag* group" characterized by a 40 chromosome karyotype. However, our sample appears characterized by a somewhat longer tail and, possibly, a longer hindfoot (but KLEIN et al. [1975] did not indicate precisely whether they included the claw in their measurement). Concerning the Algerian specimens, our results also correspond to the range of variation indicated by KOWALSKI and RZEBIK-KOWALSKA (1991), the latter being so large that one may suspect that young individuals were included in the sample considered by these authors.

For all these measurements, the sample of *G. pyramidum* from Egypt (OSBORN and HELMY 1980) reaches the highest values, the specimens of *G. p. pyramidum* from the Nile Valley being the largest of all.

Table 1. Body measurements (in mm) of samples of large-sized, hairy-footed gerbils from Northern and Saharo-Sahelian Africa, often referred to as *G. pyramidum*. TL = Total length; HB = Head and body length; Hf = Hindfoot length; E = Ear length. The sample from Egypt includes *G. p. pyramidum*, *G. p. gedeedus* and *G. p. elbaensis*.

	TL	HB	T	Hf	E	Reference
G. p. tarabuli type		105	149	30 (s. u.)	15	THOMAS (1902)
G. riggenbachi type		101	132	30 (s. u.)	13	THOMAS (1903)
G. pyramidum Senegal (n = 1)		122	156	34	14	HUBERT and BÖHME (1978)
Gerbillus sp. ("agag" group) Mauritania (n = 46)		91–117	123–148	26–29	12–16	KLEIN et al. (1975)
Gerbillus sp. Mauritania (n = 27)		89–108	134–161	27–31	13–16	This study
G. pyramidum Algeria (n = 83–87)	200–274		110–172	25–32	13–17.5	KOWALSKI and RZEBIK-KOWALSKA (1991)
Gerbillus sp. Algeria (n = 14)		80–110	130–150	28–35	12–15	This study
G. pyramidum Tunisia (n = 30)	222–267		124–149	27–35	13–17	JORDAN et al. (1974)
G. p. tarabuli Lybie (n = 31)	246–289		132–165	30–35	14–17	RANCK (1968)
G. p. tibesti Tchad (n = 15)	258–300		146–176	32–37	15–18	SETZER and RANCK (1971)
G. pyramidum, Egypte (n = 60–70)		102–135	128–180	30.5–39	14–20	OSBORN and HELMY (1980)
G. pyramidum, Sudan (n = 5)		97–121	125–149	28.3–30	11.9–16.1	TAWILL and NIETHAMMER (1989)

Table. 2. Skull measurements (in mm) of samples of large-sized, hairy-footed gerbils from Northern and Saharo-Sahelian Africa, often referred to as *G. pyramidum*. See text for abbreviations, explanation, and table 1 for references.

	ONL	CBL	ZW	NL	IOB	D	PFL	UMR	BCW	B
G. tarabuli type	32.7	25	17.2	13	6.6	9	6	4		
G. riggenbachi type	31	33 (sic)	16.2	12	6.5	8.5		4	14	10.2
G. pyramidum Senegal (n = 1)	34.8		19.1		6.1			4.8		9.3
Gerbillus sp. ("agag" group) Mauritania (n = 46)	28.6–32.4							3.5–4.3		
Gerbillus sp. Mauritania (n = 27)	29.4–31.7	26.3–20.0	15.7–17.5		5.6–6.3	7.5–8.9	4.7–5.6	3.5–4.2	13.6–14.4	8.6–9.9
G. pyramidum Algeria (n = 83–87)		24.8–31.2	14.8–18.2		5.3–7.0			3.9–4.9		
Gerbillus sp. Algeria (n = 10–12)	30.8–34.7	27.2–31.3	16.5–18.7		5.9–6.7	7.6–9.1	4.9–5.8	4.1–4.5	13.7–15.0	9.5–10,6
G. pyramidum Tunisia (n = 30)	29.5–34.5	25.9–30.9	15.6–19.0		5.7–6.9		3.8–4.8	4.4–5.9	14.1–15.4	10.2–12.6
G. pyramidum tarabuli Lybia (n = 31)	31.8–35.6		16.7–18.6	12.4–14.3	6.3–7.4			3.9–4.5		11.2–12.3
G. p. tibesti Tchad (n = 15)	31.5–35.2		16.7–18.7	12.4–14.6	5.9–7.1			3.8–4.3		11.5–12.7
G. pyramidum, Egypte (n = 60–73)	32.5–38.1		16.8–20.8	12.5–15.5	6.0–7.4		5.2–6.4	4.5–5.5	14.5–16.3	9.2–11.5
G. pyramidum, Sudan (n = 4)	31.2–34.4	26.8–33.7	16.6–17.6				5.3–6.0		15.0–16.0	

Discussion

A karyotype with 2 n = 40, NFa = 74, comprising 18 pairs of submetacentric to metacentric and one small pair of acrocentric autosomes has already been presented for large-sized, hairy-footed gerbils from Senegal (Hubert and Böhme 1978; Granjon et al. 1992), Morocco (Lay et al. 1975), and Tunisia (Jordan et al. 1974; Chibani and Lamine-Cheniti 1982). Earlier drawings of the chromosomes of Algerian specimens by Matthey (1952) are more difficult to interpret, but most probably represent the same pattern. The X chromosome appears as a relatively large submetacentric and the Y chromosome as a middle sized submetacentric in Lay et al. (1975), whereas both sex chromosomes appear as metacentrics slightly different in size in Jordan et al. (1974). In all instances, two relatively large pairs of submetacentric chromosomes characterized by very small short arms are clearly visible, but the number of other pairs identified as submetacentrics varies from 5 (Jordan et al. 1974) to 9 (Lay et al. 1975). However, the absence of chromosome banding in these studies makes it difficult and somewhat arbitrary to identify chromosome morphology unambiguously (metacentric vs submetacentric, or submetacentric vs subtelocentric). Slightly different arrangements and interpretations of these karyotypes can be done, resulting in figures very similar to the ones we obtained in the specimens from Mauritania and Algeria that we studied. Awaiting further data, these similarities suggest a more or less complete homology between the 2 n = 40 karyotypes reported from all these countries, a fact that was proven here between the specimens from Mauritania and Algeria by virtue of high resolution banding techniques.

On the other hand, the karyotype of specimens from Egypt as shown in Wassif et al. (1969) and Lay et al. (1975) is characterized by 38, all meta- to submetacentric chromosomes. Four pairs are considered to be submetacentric by Lay et al. (1975), among which not one appears to have particularly short arms. The same may be true in the specimens from Sudan studied by Tawil and Niethammer (1989), who described the chromosomes to be all metacentric or submetacentric, but no photograph of the karyotype was provided in this study. Moreover, many other chromosomes are clearly distinct in size and morphology from those figured in karyotypes with 2 n = 40. This means that at least some of them are rearranged differently between the two karyotypes (2 n = 38 and 2 n = 40). For instance, the absence of acrocentric pairs in 2 n = 38 chromosome gerbils is most probably the result of a tandem translocation, a chromosomal rearrangement known for its strongly negative heterotic effect in the heterozygous state (Wright 1982). Finally, the comparison of G-, R- and C-banded sex chromosomes of *G. pyramidum* (see Fig. 2 in Wahrman et al. 1983, where unfortunately chromosome banding data were not presented for autosomes) with those of the 2 n = 40 individuals presented here, shows clear differences.

It appears finally that there is probably more than a simple difference of one pair of small acrocentric chromosomes (that could be explained by one single event) between the 2 n = 38 and 2 n = 40 karyotypes. This difference needs to be more accurately documented, which will be possible once 2 n = 38 specimens are studied by high resolution banding techniques. Nevertheless, the rearrangements suggested by the comparison made above constitute a strong argument for considering the specimens characterized by these two karyotypes as belonging to two distinct species. The eastern, 2 n = 38, one corresponds to *G. pyramidum*, the type specimen of which was collected in the surroundings of the Great Pyramids in Egypt, and which would range along the Nile Valley, in Egypt, and Sudan, and in the oases of the region as proposed by Musser and Carleton (1993). On the other hand, the apparent homogeneity of the 2 n = 40 chromosome karyotype from Northern Senegal in the West eastwards to Tunisia suggests that the corresponding specimens may belong to only one species. *G. riggenbachi* was described by Thomas (1903) from Rio de Oro, a coastal site on the Tropic of Cancer which is some 350–400 km distant

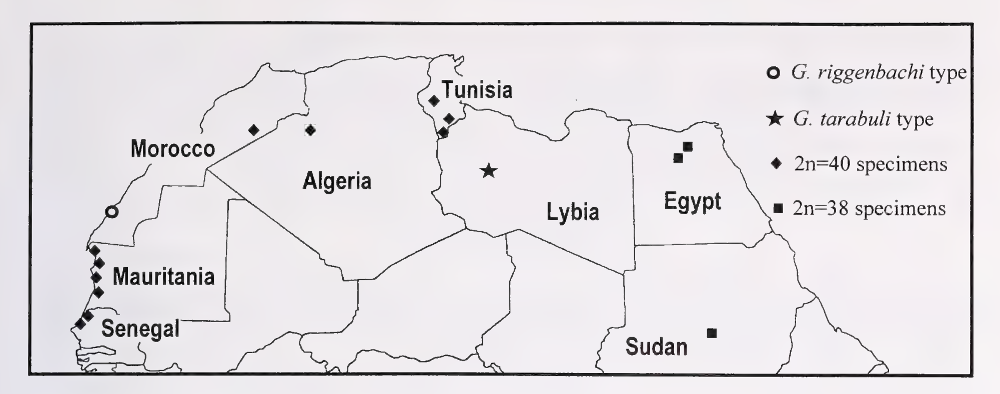


Fig. 3. Map of northern Africa, showing localities where 2 n = 40 and 2 n = 38 chromosome specimens of *Gerbillus* have been recorded, and type-localities of *G. riggenbachi* and *G. tarabuli.*

from the site where the specimens from Northern Mauritania chromosomally analysed here originated (Fig. 3). *G. pyramidum tarabuli* was described by the same author one year earlier, on the basis of specimens caught in various localities of central West and the coastal North of Libya (Thomas 1902). A number of these localities, including Sebha, from which the type specimen was caught, are situated 550 to 600 km east from south-eastern Tunisia (Fort Saint), where Jordan et al. (1974) reported specimens with 40 chromosomes (Fig. 3). Although the whole region can be environmentally subdivided in a number of ways (see, for instance the climatic and phytogeographic subdivisions presented by Le Houerou (1992), an arid to semi-arid nucleus has persisted at least throughout the Pleistocene and Holocene in the lowlands along the Tropic of Cancer, which extension has varied according to climatic changes (Le Houerou 1992). The absence of a significant north-south barrier between the western coast and the Libyan desert is another argument to support the existence of one wide-ranging species of large-sized, hairy-footed gerbil characterized by the 2 n = 40, NFa = 74 karyotype described here. Contrary to Lay (1983, followed by Musser and Carleton 1993), we thus propose to abandon *G. riggenbachi* as a valid species and, for reasons of priority, to consider only *G. tarabuli* as being present in this region. Its distribution would range, more or less continuously, from northern Senegal in the west (Duplantier et al. 1991) to the Cyrenaican Plateau of Libya (Ranck 1968) and the Tibesti Mountains of Chad (Setzer and Ranck 1971) in the east. The hiatus in *G. pyramidum* distribution mentioned by Ranck (1968) in eastern Libya and western Egypt, corresponding to the Cyrenaican Plateau and the northern part of the Libyan desert may well represent the barrier that has been at the origin of the differentiation between *G. pyramidum* and *G. tarabuli.*

The morphological and biometrical data appear of relatively little value for a priori characterization of these species. Specimens of *G. pyramidum* from Egypt can reach a larger size than that of specimens from the other origins but the biometrical characteristics of the series from Sudan fall in the range of the values obtained for other samples. Conversely, significant differences can be evidenced between samples of *G. tarabuli* from various origins (as here between the samples from Mauritania and Algeria). This apparently important morphometrical variability within both *G. pyramidum* and *G. tarabuli* is probably related to eco-climatological variations of the environment in which these populations live (see Petter 1961), and would deserve further analyses. The proposal of Lay et al. (1975) to consider *G. riggenbachi* as a distinct species, following comparison of museum specimens, has never been substantiated, and would need to be critically examined on the basis of large-scale analyses, taking into account this environmentally and geo-

graphically determined variability. Meanwhile, it seems important to gather as much chromosomal information as possible on these gerbils from all over North Africa, in an attempt to map more precisely their distribution. The establishment of diagnostic morphological characteristics could then be envisaged, to determine whether splitting of what we propose to call *G. tarabuli* is justified.

Acknowledgements

We are grateful to M. Lombard for technical assistance. We also thank F. Colas and A. T. Dia, heads of the project "Biodiversité du littoral mauritanien", financed by the European Commission, during which the specimens from Mauritania were caught, with the help of J.-F. Cosson, J. Cuisin, and M. Tranier. Thanks go also to J.-F. Voisin for the German version of the abstract. This is contribution no. 99-2 from EA 2586.

Zusammenfassung

Neubewertung der taxonomischen Stellung nordafrikanischer Rennmäuse, die gewöhnlich Gerbillus pyramidum (Gerbillinae, Rodentia) zugeschrieben werden: Chromosomale und biometrische Daten

Es wurden die chromosomalen und biometrischen Characteristika großer, nordafrikanischer Rennmäuse untersucht, die gewöhnlich dem Taxon *Gerbillus pyramidum* zugeschrieben werden. Hochauflösende Bänderungstechniken zur Chromosomenanalyse wie auch verschiedene Körper- und Schädelmaße wurden zum Vergleich von Tieren aus Mauretanien und Algerien herangezogen. Alle untersuchten Rennmäuse zeigten den gleichen, durch 40 Chromosomen und 74 autosomale Arme gekennzeichneten Karyotyp. Rennmäuse aus Algerien waren generell größer als jene aus Mauritanien. Vergleiche mit den publizierten Angaben über Rennmäuse aus anderen nordafrikanischen Ländern (Senegal, Marokko, Tunesien) legen nahe, daß alle zuvor beschriebenen $2n = 40$ Karyotypen dieselbe Spezies repräsentieren, welche sich chromosomal deutlich von den Individuen mit $2n = 38$ abhebt, die in Ägypten und im Sudan zu finden sind und dem echten *Gerbillus pyramidum* entsprechen. Nach unseren Ergebnissen schlagen wir vor, daß die von Senegal bis Lybien gefundenen Exemplare mit $2n = 40$ einer einzigen Art entsprechen, welche den Namen *Gerbillus tarabuli* tragen sollte. Diese, im nördlichen Afrika weitverbreitete Art zeigt ein anscheinend breites Spektrum an biometrischer Variabilität, die mit der Variabilität des Lebensraums zu tun haben könnte.

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Z. Säugetierkunde **64** (1999) 308–318

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Spatial partitioning of allozyme variability in European mountain hares (*Lepus timidus*): gene pool divergence across a disjunct distributional range?

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Receipt of Ms. 19. 04. 1999
Acceptance of Ms. 28. 07. 1999

Abstract

To investigate if the postglacial dispersion of mountain hares (*Lepus timidus*) into the present geographically separated ranges in Europe has produced marked gene pool differentiation, 209 individuals from Scandinavia, Russia, the Alps, Scotland, and Ireland were screened for allozymic variability at 40 structural gene loci by horizontal starch gel electrophoresis. Polymorphisms were detected at 13 loci. Most alleles were identical with those of brown hares (*Lepus europaeus*) studied earlier in Europe. Average expected heterozygosity (2.0–5.0 %) and rates of polymorphism (8.8–29.4 %) in regions or subspecies were comparable to those of local samples of European brown hares studied earlier. Despite a high amount (31.3 %) of "private alleles", genetic distances (Nei's 1978 D: 0.000–0.008 among subspecies, and 0.000–0.017 among regions) were similar to those found among local samples of central European brown hares. This indicates low genetic differentiation among gene pools of subspecies or regions. Also, relatively low mean F_{ST} values (0.157 for regions, 0.14 for subspecies) and low numbers of significantly differing allele frequencies indicated little genetic differentiation. Wright's (1978) hierarchical F-statistics revealed that less than 1 % of the relative genetic variation was partitioned among subspecies but 13.6 % among regions within subspecies. All results conform to the hypothesis of a quite panmictic gene pool of late-glacial and postglacial mountain hares in Europe. They also support the view that no severe drift has occurred in postglacial populations during the colonization of the present ranges.

Key words: *Lepus timidus*, allozymes, colonization, genetic differentiation, disjunct distribution

Introduction

Mountain hares (*Lepus timidus*) have a disjunct distribution in Europe, with natural ranges in the subarctic/arctic regions of Russia and Fennoscandia, the Baltic region and Poland, the Alps, Scotland, and Ireland. Mountain hares from these regions are considered separate subspecies (*L. t. timidus*, *L. t. kozhevnikovi*, *L. t. sylvaticus*, *L. t. varronis*, *L. t. scoticus*, *L. t. hibernicus*), mainly due to morphometric differences and pelage coloration (see Angerbjörn and Flux 1995). According to late Pleistocene and early Holocene

0044-3468/99/64/05 – 308 $ 12.00/0

ecotopes, geography, and fossil records (e.g., LANG 1994; STUART 1982; DÖPPES 1997; see also CORBET 1986), however, this hare species was most probably continuously distributed over large parts of Europe between the northern and the Alpine ice sheets by the end of the last glaciation period (at 10.000–12.000 YBP). Apparently, they were hunted by Magdalénien Cro-Magnon people of central Europe (e.g., DÖPPES 1997).

This study addresses the degree of cross gene pool differentiation among the currently spatially well separated subspecies of European mountain hares. Provided the late Pleistocene population of mountain hares did exhibit a panmictic gene pool across large parts of central and north-central Europe, rather than an already substructered one, and no severe or long lasting demographic bottlenecks ("founder effects" etc.) have occurred during the postglacial colonization of the present ranges, we should expect a low gene pool differentiation among the currently acknowleged subspecies in Europe. Alternatively, a possible structuring of the late glacial gene pool into regional populations and/or strong genetic drift during the post-glacial colonization period might have led to signifcant genetic differences among the subspecies in Europe.

Material and methods

A total of 209 mountain hares was collected at diverse localities in the Alps (Switzerland, France, Austria), Scandinavia, the Ural mountains (Russia), Scotland (U.K.), the Irish Republic, and Northern Ireland (U.K.) between 1994 and 1996. Detailes of sampling localities and sample sizes are given in figure 1. These hares can be allocated to four nominal subspecies: *L. t. timidus* (Scandinavia, Ural), *L. t. varronis* (Alps), *L. t. scoticus* (Scotland), and *L. t. hibernicus* (Ireland). The sample from Scotland (Mull) may also include the subspecies *L. t. hibernicus*, or *L. t. scoticus* × *L. t. hibernicus* hybrids because of the introduction of this subspecies to Mull in the last century (CORBET and SOUTHERN 1977; see also FLUX 1970 for mountain hares from mainland Scotland). Among the presently studied mountain hares from Sweden (*L. t. timidus*) introgression of *L. t. sylvaticus* cannot be entirely excluded. The Swedish hares were shot in January/February but unfortunately the hunters did not make any special remarks as to blue/grey coat colour which is typical for *L. t. sylvaticus* (BERGENGREEN 1969).

Sexing of hares was carried out by inspection of their internal reproductive organs. Age (adult vs. juvenile/subadult) was estimated by body size, body weight, and by checking for the occurrence of the lateral epiphyseal protrusion of the ulna; the latter method separates juveniles/subadults (born in the last reproductive season) from older ones (WALHOVD 1965).

The following 25 isozymes/-systems encoded by 40 hypothetical structural gene loci were assayed for allozymic variation by horizontal starch gel electrophoresis (isozyme/-system, abbreviation, E.C. number, and corresponding structural gene loci in parentheses): alpha-glycerophosphate dehydrogenase (GDC, 1.1.1.8, Gdc), sorbitol dehydrogenase (SDH, 1.1.1.14, Sdh), lactate dehydrogenase (LDH, 1.1.1.27, Ldh -1, -2), malate dehydrogenase (MOR, 1.1.1.37, Mor -1, -2). malic enzyme (MOD, 1.1.1.40, Mod -1, -2), isocitrate dehydrogenase (IDH, 1.1.1.42, Idh -1, -2), 6-phospho-gluconate dehydrogenase, (PGD, 1.1.1.44, Pgd), glutamate dehydrogenase (GLUD, 1.4.1.3, Glud), catalase (CAT, 1.11.1.6, Cat), superoxide dismutase (SOD, 1.15.1.1, Sod -1, -2), purine nucleoside phosphorylase (NP, 2.4.2.1, Np), aspartate amino-transferase (AAT, 2.6.1.1, Aat -1, -2), hexokinase (HK, 2.7.1.1, Hk -1, -2, -3), creatine kinase (CK, 2.7.3.2, Ck -1, -2), adenylate kinase (AK, 2.7.4.3, Ak -1, -2), phospho-glucomutase (PGM, 2.7.5.1, Pgm -2, -3), esterases (ES, 3.1.1.1, Es -1; ES-D, 4.2.1.1, Es-D), acid phosphatase (ACP, 3.1.3.2, Acp -1), fructose-1,6-diphosphatase (FDP, 3.1.3.11, Fdp-1), β-galactosidase (β-GAL, 3.2.1.23, β-Gal), peptidases (PEP, 3.4.11, Pep -1, -2), fumarate hydratase (FH, 4.2.1.2, Fh), aconitase (ACO, 4.2.1.3, Aco -1, -2), mannose phosphate isomerase (MPI, 5.3.1.8, Mpi), glucose phosphate isomerase (GPI, 5.3.1.9. Gpi -1, -2).

Tissue preparation, electrophoresis and protein-specific staining followed GRILLITSCH et al. (1992). Allelic variants were resolved by direct side-by-side comparison of migrating allozymes, including five brown hares (*Lepus europaeus*) on the same gels. For designation of alleles we used the nomenclature of GRILLITSCH et al. (1992). Genotypes at polymorphic loci were determined in each specimen according to the principles of enzyme electrophoresis (e.g., RICHARDSON et al. 1986; ROTHE 1994). In several individuals, however, genotypes could not be determined for the entire set of loci due to insufficient

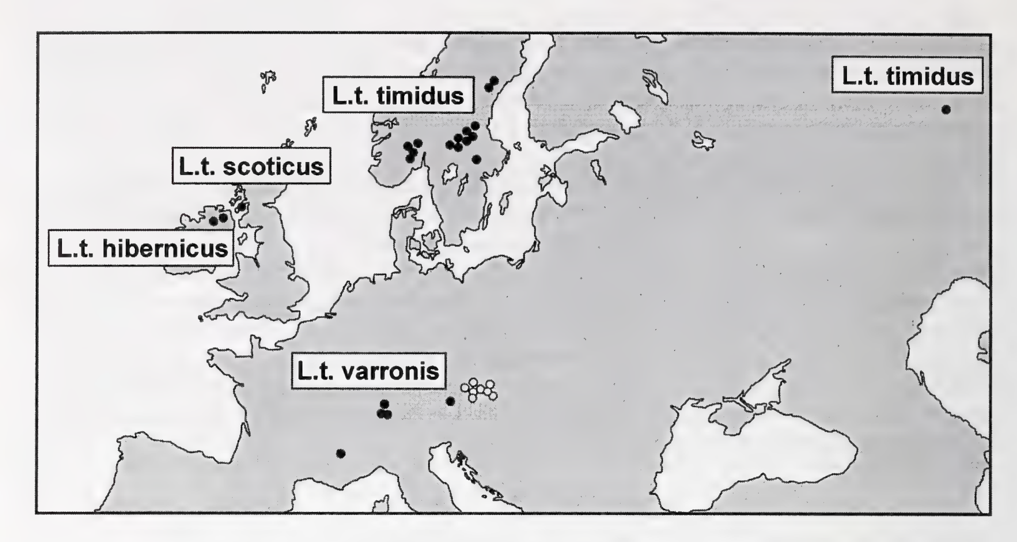


Fig. 1. Sampling locations of mountain hares (full circles) and associated subspecies names. Sample sizes in parentheses. Switzerland: canton Grisons, central and northern parts (49); Engadin (23); Val Mesolcina, Val Calanca, Val Bregaglia, Val Poschiavo (15); canton Glarus (16); Austria: Hohe Tauern (4); France: St. Véran (3); Abriès (3); Châteauroux (1); Aiguilles (1); Sweden: Jämtland (22); Växvik region (6); Väster- and Norbotten (7); Uppland (7); Norway: Ringebu (19); South Norway (5); Telemark (5): Russia: Polevskoy, Ural (14); Scotland (U. K.): Mull (5); Northern Ireland (U. K.): Autrim (1); Tyrone (1); Rep. Ireland: Mayo (1); Sligo (1). Open circles: Local populations of brown hares (*Lepus europaeus*) from Austria (cf., HARTL et al. 1993) used for comparison of genetic differentiation.

quality of resolution producing ambiguous interpretations. All population genetic statistics regarding regional samples of *L. timidus* and the comparison of *L. timidus* regional samples and the *L. europaeus* local samples were based on 40 loci. For the comparison of *L. timidus* subspecies all analyses were based on 34 loci (omitting the Mor-2; Ck-1, -2; Pgi; Cat; Gdc loci) because of total lack of data for these loci in certain subspecies.

Allele frequencies were calculated by using the BIOSYS-1 pc package 1.7 (SWOFFORD and SELANDER 1989). Allele frequencies of hares from Switzerland were tested for independence of age class (young of the year vs. older animals) or sex by Fisher's exact tests (using SPSS). Association of genotypes between loci was also tested by Fisher's exact tests for each pair of polymorphic loci with aggregated genotypes to check for linkage disequilibrium. Significance was based on sequential Bonferroni procedures (with a nominal alpha = 0.05) to account for multiple testing (RICE 1989). Allele frequencies at single loci were tested for significant variation between pairs of regions and pairs of subspecies by Fisher's exact tests of aggregated alleles in cases of more than two alleles per locus and sequential Bonferroni procedure.

The BIOSYS-1 pc package, release 1.7 (SWOFFORD and SELANDER 1989) was also used to calculate the rate of polymorphism (P, 99 % criterion), the mean number of alleles per locus (A), and mean heterozygosities (H_e-expected, H_o-observed) for each regional, subspecies, and local sample. It was further employed to calculate WRIGHT's (1978) non-hierarchical and hierarchical F-statistics. The latter was calculated to test for partitioning of genetic variability among subspecies relative to partitioning among regions within subspecies. NEI's (1978) genetic distances, corrected for small sample sizes, ROGERS' (1972) distances and modified ROGERS' distances (WRIGHT 1978) between all pairs of regional and subspecies samples of mountain hares and local samples of brown hares were calculated. Regarding brown hares, eight local samples studied earlier in the same laboratory (HARTL et al. 1993) were used with adjusted numbers of loci (n = 40). Relationships of pairwise genetic distances were revealed by an unrooted Wagner dendrogram (FARRIS 1972).

Results

Polymorphism was revealed at 13 loci. The overall rate of polymorphism (99 % criterion, 40 loci considered) for European mountain hares amounted to 32.5 %. Polymorphic loci, alleles, and associated allele frequencies are given in table 1 for four regions of Europe (disregarding subspecific allocation), and in table 2 for subspecies. Allele frequencies of mountain hares from Switzerland did not vary significantly among age classes or sexes. Values of

Table 1. Allele frequencies (%) at polymorphic loci of mountain hares from four regions of Europe based on 40 loci. H_o = average observed heterozygosity, H_e = average expected heterozygosity, P = rate of polymorphism (99% criterion), A = mean number of alleles per locus. Significant deviations of genotype frequencies from expected Hardy-Weinberg frequencies are indicated for respective loci and regions ([a] $p < 0.05$; [b] $p < 0.01$, significance tests using exact probabilities).

Subspecies Locus	Allele	Scandinavia (n = 74) *L. t. timidus*	Alps (n = 112) *L. t. varronis*	Ural (n = 14) *L. t. timidus*	NW Europe (n = 9) *L. t. scoticus* and *L. t. hibernicus*
Sdh	a	0.000	0.041[b]	0.000	0.111
	b	1.000	0.959	1.000	0.889
β-Gal	a	0.000	0.016	0.400[b]	0.000
	b	1.000	0.964	0.600	0.100
	c	0.000	0.020	0.000	0.000
Ldh-2	a	1.000	1.000	1.000	0.889
	d	0.000	0.000	0.000	0.111
Idh-2	a	0.831[a]	0.925	0.321	1.000
	d	0.169	0.071	0.679	0.000
Pgd	a	1.000	1.000	0.964	1.000
	b	0.000	0.000	0.036	0.000
Hk-2	a	0.973	1.000	1.000	1.000
	b	0.027	0.000	0.000	0.000
Es-1	a	0.143[b]	0.100	0.143	0.071
	b	0.843	0.900	0.857	0.786
	c	0.000	0.000	0.000	0.143
	e	0.014	0.000	0.000	0.000
Es-D	a	0.810	0.887	0.929	0.688
	b	0.148	0.113	0.071	0.312
	c	0.042	0.000	0.000	0.000
Pep-2	a	0.036	0.054	0.000	0.000
	b	0.906	0.922	1.000	1.000
	c	0.058	0.024	0.000	0.000
Acp-1	a	0.000	0.036[b]	0.000	0.000
	b	1.000	0.964	1.000	1.000
Mpi	a	0.948	0.964	0.929	0.938
	b	0.052	0.014	0.071	0.062
	c	0.000	0.022	0.000	0.000
Acon	a	0.979	0.986	1.000	1.000
	b	0.021	0.014	0.000	0.000
Me-2	a	1.000	1.000	0.929[a]	1.000
	b	0.000	0.000	0.071	0.000
H_o		0.026	0.021	0.025	0.034
H_e		0.031	0.024	0.041	0.032
P		17.5	22.5	17.5	12.5
A		1.3	1.3	1.2	1.1

Table 2. Allele frequencies (%) at polymorphic loci of four subspecies of mountain hares from Europe based on 34 loci. H_o = average observed heterozygosity, H_e = average expected heterozygosity, P = rate of polymorphism (99 % criterion), A = mean number of alleles per locus. Significant deviations of genotype frequencies from expected Hardy-Weinberg frequencies are indicated with the "a" allele for respective loci and subspecies ([a] p<0.05; [b] p<0.01, significance tests using exact probabilities).

Subspecies Locus	Allele	*L. t. timidus* (n = 88)	*L. t. varronis* (n = 112)	*L. t. scoticus* (n = 5)	*L. t. hibernicus* (n = 4)
Sdh	a	0.000	0.041[b]	0.100	0.125
	b	1.000	0.959	0.900	0.875
β-Gal	a	0.103[b]	0.016	0.000	0.000
	b	0.897	0.964	1.000	1.000
	c	0.000	0.020	0.000	0.000
Ldh-2	a	1.000	1.000	1.000	0.750
	d	0.000	0.000	0.000	0.250
Idh-2	a	0.774[b]	0.929	1.000	1.000
	d	0.256	0.071	0.000	0.000
Pgd	a	0.994	1.000	1.000	1.000
	b	0.006	0.000	0.000	0.000
Hk-2	a	0.977	1.000	1.000	1.000
	b	0.023	0.000	0.000	0.000
Es-1	a	0.143[a]	0.100	0.000	0250
	b	0.844	0.900	0.800	0.750
	c	0.000	0.000	0.200	0.000
	e	0.013	0.000	0.000	0.000
Es-D	a	0.829	0.887	0.900	0.333
	b	0.135	0.113	0.100	0.667
	c	0.035	0.000	0.000	0.000
Pep-2	a	0.030	0.054	0.000	0.000
	b	0.922	0.922	1.000	1.000
	c	0.048	0.024	0.000	0.000
Acp-1	a	0.000	0.036[b]	0.000	0.000
	b	1.000	0.964	1.000	1.000
Mpi	a	0.944	0.964	1.000	0.833
	b	0.056	0.014	0.000	0.167
	c	0.000	0.022	0.000	0.000
Acon	a	0.983	0.986	1.000	1.000
	b	0.017	0.014	0.000	0.000
Me-2	a	0.989[b]	1.000	1.000	1.000
	b	0.011	0.000	0.000	0.000
H_o		0.030	0.025	0.024	0.066
H_e		0.044	0.029	0.020	0.050
P		29.4	26.5	8.8	14.7
A		1.4	1.4	1.1	1.1

genetic variability for the regions (based on 40 loci) are listed in table 1, and for the subspecies (based on 34 loci) in table 2. The observed genotypic distributions differed significantly from Hardy-Weinberg expectations at six loci in three regional samples (Tab. 1) and at six loci in two subspecies samples (Tab. 2). Basically, all these significant genotype deviations were due to heterozygote deficiencies. Pairwise NEI's (1978) genetic distances in mountain hares, corrected for small sample sizes, ranged between 0.000–0.008 among subspecies, and between 0.000–0.017 among regions (Tab. 3). Modified Rogers' distances (WRIGHT 1978) ranged between 0.037–0.117 among subspecies, and between 0.024–0.135 among regions (Tab. 3). Pairwise genetic distances between single regional samples of mountain hares and

single local samples of central European brown hares ranged between 0.068–0.093 (NEI's 1978 D), and between 0.253–0.295 (Rogers' modified distances; WRIGHT 1978).

In mountain hares, locus-specific F_{ST} and F_{IS} values did not show any particular concordance across loci; for the regional samples mean $F_{ST} = 0.157$, mean $F_{IS} = 0.17$, and mean $F_{IT} = 0.3$. For the subspecies samples the respective values were 0.14, – 0.02, and 0.12. The relative genetic differentiation (F_{ST} values) for pairs of subspecies are listed in table 4 along with associated significances of heterogeneity of allele frequencies. Only

Table 3. NEI's (1978) genetic distances for small sample sizes (above diagonal) and modified Rogers' distances (below diagonal) among pairs of mountain hares from European regions (based on 40 loci), and subspecies (based on 34 loci). Regions: SCAN = Scandinavia, ALPS, URAL, NWE = Northwest Europe (Scotland, Ireland).

	SCAN (1)	ALPS (2)	URAL (3)	NWE (4)	*L. t. timidus* (5)	*L. t. varronis* (6)	*L. t. scoticus* (7)	*L. t. hibernicus* (8)
(1)	–	0.000	0.010	0.001				
(2)	0.024	–	0.013	0.001				
(3)	0.106	0.115	–	0.017				
(4)	0.049	0.047	0.135	–				
(5)					–	0.001	0.003	0.008
(6)					0.039	–	0.000	0.008
(7)					0.062	0.037	–	0.007
(8)					0.115	0.113	0.117	–

Table 4. F_{ST} values for pairs of subspecies (above diagonal) and significance values for heterogeneity of allele frequencies (below diagonal); significance is based on exact Fisher's test and sequential Bonferroni procedure (sig.: $p < 0.05$; n.s.: $p > 0.05$). Significance is given with significantly varying allele frequencies at least at one locus.

	L. t. timidus (1)	*L. t. varronis* (2)	*L. t. scoticus* (3)	*L. t. hibernicus* (4)
(1)	–	0.02	0.056	0.123
(2)	sig.	–	0.028	0.139
(3)	n. s.	n. s.	–	0.164
(4)	sig.	sig.	n. s.	–

Table 5. F_{ST} values for pairs of sampling regions of *L. t. varronis* and *L. t. timidus*, respectively (above diagonal), and significance values for heterogeneity of allele frequencies (below diagonal), based on exact Fisher's test and sequential Bonferroni procedures (sig.: $p < 0.05$; n.s.: $p > 0.05$). Significance is given if at least one locus shows significantly varying allele frequencies in a pairwise comparison.

L. t. varronis		(1)	(2)	(3)	(4)	(5)
	Switzerland (1)	–	0.146	0.048	0.173	0.014
	Austria (2)	n. s.	–	0.055	0.237	0.107
	France (3)	n. s.	n. s.	–	0.171	0.024
L. t. timidus						
	Ural (4)	sig.	n. s.	sig.	–	0.135
	Scandinavia (5)	n. s.	n. s.	n. s.	sig.	–

6.8 % of all possible pairwise comparisons of region-specific allele frequencies at polymorphic loci (59 tests) yielded significant differences. According to theory, significance of pairwise F_{ST}-values is given with allele frequencies varying significantly at least at one locus studied (WRIGHT 1978). F_{ST}-values for pairs of sampling regions within the subspecies *L. t. timidus* and *L. t. varronis*, respectively, as well as associated significance values for heterogeneity of allele frequencies are given in table 5. Significant differences of allele frequencies at polymorphic loci were found only in 5.4 % of all possible pairwise comparisons between regions (92 tests). Details of WRIGHT's (1978) hierarchical F-statistics giving the proportions of genetic variation partitioned among the four subspecies studied, relative to the regional effect on genetic partitioning, is presented in table 6. An unrooted Wagner dendrogram based on Rogers' distances, depicting genetic relationships among mountain hares from the four regions studied in Europe and eight local samples of brown hares from central Europe (HARTL et al. 1993) is presented in figure 2.

Table 6. Wright's hierarchical F-statistics in European mountain hares, based on 34 allozyme loci. Variance components and F-statistics combined across loci.

Comparison X – Y	variance component	F_{XY}
sampling regions[1]–subspecies	0.2096	0.129
sampling regions[1]–total variance	0.2230	0.136
subspecies–total variance	0.0134	0.008

[1] Austria, France, Ireland, Scandinavia, Scotland, Switzerland, Ural.

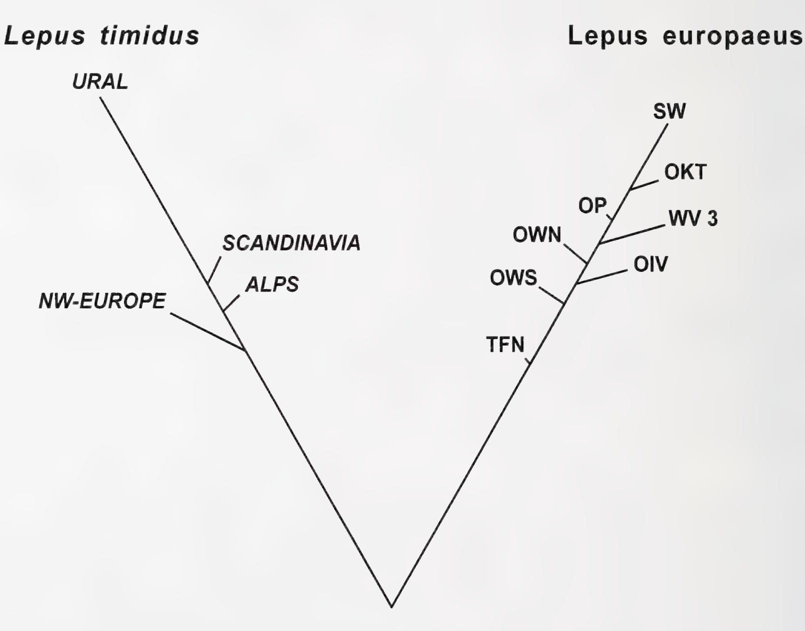


Fig. 2. Unrooted Wagner dendrogram (midpoint rooting of longest path) depicting genetic relationships among mountain hares (*Lepus timidus*) from various regions of Europe and brown hares (*L. europaeus*) from eight local samples of central Europe. The dendrogram is based on ROGERS' (1972) distances, calculated from allele frequencies at 40 loci. Total tree length = 0.192, distance between "Ural" and "Scandinavia" = 0.032, cophenetic correlation coefficient = 0.986

Discussion

The level of gene pool variability of European mountain hares, as indicated by allozyme heterozygosity, rate of polymorphism, and mean number of alleles per locus in the diverse regions and subspecies is similar to that of brown hares from various continental European regions (HARTL et al. 1989, 1990, 1992, 1993, 1995; SUCHENTRUNK et al. 1998, 1999). The presently found heterozygosity values are typical for undisturbed populations of terrestrial mammalian species of diverse orders (NEVO 1978; TIEDEMANN et al. 1996). The somewhat reduced rates of polymorphism and mean numbers of alleles per locus in Scottish and Irish mountain hares are likely due to the low sample sizes. The $H_e : P$ rates within regions and subspecies ranged between 0.107–0.256. These values fall within the range of "undisturbed" populations (TIEDEMANN et al. 1996), indicating populations without genetic depletion e. g., due to severe bottlenecks or long-term low effective population size. Average numbers of alleles per locus (A) do not give any hint for depauperated gene pools in Scandinavia, the Ural or the Alps. The low A-values for mountain hares from Scotland and Ireland are most probably due to the low sample sizes for these regions.

The overall rate of polymorphism of the mountain hares (32.5 %) appears to be somewhat greater than in brown hares. Combining the data of HARTL et al. (1989, 1990, 1992, 1993, 1994, 1995) and SUCHENTRUNK et al. (1998, 1999) for brown hares from various regions of Europe yields an overall rate of polymorphism of 25.9 %. Adjusting the set of loci analysed in brown hares to the presently studied set (40 loci) results in a value of 27.5 % for brown hares. The still somewhat higher value of mountain hares is due to three polymorphic loci (Me-2, Acp-1, Acon). But these three loci are only marginally polymorphic with variant alleles occurring in one or two regions, respectively. Furthermore, the Acp-1^a allele occasionally found in some mountain hares from Switzerland may result from rare cases of hybridization (cf. e. g., BALDENSTEIN 1863; FRAGUGLIONE 1966; SCHRÖDER et al. 1987; THULIN et al. 1997 a). In general, most of the loci found polymorphic in brown hares (HARTL et al. 1990, 1992, 1993; SUCHENTRUNK et al. 1998; 1999) are also polymorphic in the presently studied mountain hares. Moreover, most of the loci with several alleles in brown hares (Es-1, β-Gal, Pep-2, Mpi) reveal several of these alleles in the mountain hares too.

These very similar allele patterns hamper differential diagnosis by allozymes between mountain and brown hares. When comparing allozyme patterns of brown and mountain hares GRILLITSCH et al. (1992) screened only few mountain hares from one region in Austria. With that small and regionally limited sample size they obviously have missed some polymorphisms in mountain hares. Their results suggested a differential diagnosis between these two species by three loci. However, the allelic differences at the β-Gus and the Pgm-1 loci between the two species (GRILLITSCH et al. 1992) could not be proven presently because of dubious zymograms. The present results suggest that, among the array of loci screened, only the Acp-1 locus has alleles alternately fixed in the two species, with occasional cases of introgressive hybridization in mountain hares from the Alps. However, at present no allozyme data of brown hares from regions of potential introgressive hybridization are available to substantiate this hypothesis. In Scandinavian mountain hares no hint of introgressive hybridization was found presently, although THULIN et al. (1997 a) reported presence of mountain hare mtDNA in brown hares from the Upland region.

Despite the relatively high amount of "private alleles" at several loci (31.3 % of all studied loci) in various regions or subspecies of mountain hares, overall genetic distances among gene pools of the diverse regions or subspecies are generally low in magnitude. Because of their generally low frequencies, "private alleles" do not greatly influence genetic differentiation. NEI's (1978) genetic D-values among subspecies are similar to those found among local samples of brown hares within central Europe (e. g., HARTL et al. 1989, 1990, 1992, 1993). However, brown hares also exhibit low genetic differentiaton even

across large geographic distances in Europe; this indicates a rather panmictic network and a lack of discernible populations (HARTL et al. 1990; SUCHENTRUNK et al. 1999). Only mountain hares from the Ural region and Ireland show a slightly increased genetic divergence to mountain hares from the other study regions or subspecies. In Ural mountain hares this slight separation is only based on significantly increased frequencies of the *β*-Gal^{a} and the Idh-2^{d} alleles. It might e. g., result from the large geographic distance between the Ural and the other regions or indicate introgression of gene pool elements of *L. t. kozhevnikovi*. According to OGNEFF (1929) this subspecies occurs in the south Ural (near Miass) some 150 km south of the presently studied collection site. However, skull dimensions and the external features of the presently studied individuals tend to conform with those of *L. t. timidus* of various parts of European Russia, rather than with those of *L. t. kozhevnikovi* (albeit there is little morphometric differentiation between the two subspecies in Russia; see OGNEFF 1929).

The slightly raised level of genetic separation of Irish mountain hares is particularly due to changes in allele frequencies at the Es-d locus and the presence of a "private allele" (Ldh-2^{d}) with a frequency of 25 %. However, significant changes in allele frequencies between *L. t. hibernicus* and the other subspecies was only found at the Pep-2 locus. In view of the small sample size from NW Europe, and the fact that Scottish mountain hares were only screened from the isle of Mull, where Irish mountain hares had been liberated in the last century, no conclusions regarding the genetic differentiation between these two subspecies can be drawn.

The generally low level of genetic differentiation between subspecies or regions of mountain hares is also indicated by the small proportion of relative genetic variability partitioned among subspecies or regions and particularly by the low proportions of significantly varying allele frequencies between pairs of subspecies (6.8 %) or regions (5.4 %). Moreover, while 13.6 % of the relative genetic variation are partitioned among regions within subspecies, less than 1 % is partitioned between the subspecies studied. This means that gene pool divergence is greater among sampling regions within *L. t. timidus* and *L. t. varronis*, respectively, than between all studied subspecies. Hence, no distinct gene pools of the studied subspecies can be identified. Also, a single mountain hare collected in the Primorje region of Far East Sibiria analysed in our laboratory did not reveal any new allele.

All results agree with sequence data demonstrating an admixture of mtDNA haplotypes in mountain hares from Scandinavia and other parts of Europe (THULIN et al. 1997 b) without separation in clear phylogeographic units. The present allozyme results also conform to the hypothesis of a rather panmictic gene pool of late- and postglacial populations in central Europe without any specific phyletic blocks. They are also in agreement with the view that there were no severe demographic bottlenecks, founder effects, long-term low effective population sizes, multiple regional extinctions etc. in post-glacial populations during the colonization of the present ranges. Obviously, separation of postglacial European mountain hares into several geographic ranges has not resulted in distinct gene pools; and there is very little measureable evolutionary divergence between the pools of coding genes in the phenotypically specified subspecies.

Acknowledgements

We are grateful to the hunters from Grisons and Glarus (Switzerland), to the Swedish hunters, to Mr. K. KNOTT (forestry commission Oban, Scotland) and Dr. R. MAURIZIO (Vicosoprano, Switzerland) for shooting the hares and/or providing organ samples. Mr A. KÖRBER produced the figures. Dr. M. PAVLENKO (Russ. Acad. Sciences, Vladivostok) provided organ samples of a mountain hare from Far East Sibiria. Dr. M. JANOVSKY (Berne) transferred most of the Swiss samples and Dr. I. UDINA (Moscow) the Far East Sibirian sample to our laboratory.

Zusammenfassung

Räumliche Verteilung der Allozymvariabilität bei europäischen Schneehasen (Lepus timidus): Genpool-Divergenz in einem disjunkten Verbreitungsgebiet?

Die Allozymvariabilität von 209 Schneehasen (*Lepus timidus*) von Skandinavien, Rußland, den Alpen, Schottland und Irland wurde mittels horizontaler Stärkegelelektrophorese von 40 Strukturgenloci festgestellt, um zu prüfen, ob die postglaziale Besiedelung der heutigen disjunkten Schneehasen-Verbreitung in Europa zu einer markanten genetische Differenzierung geführt hat. Die meisten Allele an den 13 polymorphen Loci waren identisch mit den schon früher bei europäischen Feldhasen (*L. europaeus*) gefundenen. Durchschnittliche erwartete Heterozygotie-Werte pro Region bzw. Subspecies (2,0–5,0%) sowie die Polymorphieraten (8,8–29,4 %) entsprachen denen bei Feldhasen aus früheren Untersuchungen. Trotz der hohen Rate (31,3 %) an Allelen, die ausschließlich in einzelnen Regionen oder Subspecies vorkamen, lagen die genetischen Distanzen (Nei's D: 0,000–0,008 zwischen Subspezies, 0,000–0,017 zwischen Regionen) grundsätzlich im Bereich jener Werte, wie sie zwischen lokalen Feldhasen-Populationen in Mitteleuropa früher festgestellt wurden. Ebenso zeigten die relativ geringen mittleren F_{ST} Werte (0,157 zwischen Regionen; 0,14 zwischen Subspecies) sowie die geringe Zahl an signifikanten paarweisen Unterschieden von Allelfrequenzen eine geringe genetische Differenzierung zwischen den Regionen bzw. Subspecies an. Während 13,6 % der relativen genetischen Variabilität zwischen Regionen innerhalb von Subspecies verteilt waren, lag der entsprechende Wert für die Verteilung zwischen den Subspecies unter einem Prozent. Alle Ergebnisse entsprechen der Hypothese einer panmiktischen spät- bzw. postglazialen Population in Mitteleuropa und der Annahme, daß bei der Kolonisation der heutigen disjunkten Verbreitungsgebiete in Europa keine starke genetische Drift erfolgt ist.

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Z. Säugetierkunde **64** (1999) 319–320
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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Buchbesprechungen

Wandrey, R. (1997): **Die Wale und Robben der Welt:** Vorkommen, Gefährdung, Schutz. Kosmos Naturführer. Stuttgart: Franckh-Kosmos Verlags-G.m.b.H. & Co. 285 pp., 93 Farb-, 24 s/w-Zeichnungen, 108 Farbfotos, 120 zweifarbige Verbreitungskarten. DM 49,80 / öS 364,– / sFr 47.80. ISBN 3-440-07047-6.

Dr. Rüdiger Wandrey, der Direktor des „Zoos am Meer" in Bremerhaven, hat einen schönen und instruktiven Naturführer über aquatische Säugetiere vertaßt. Der Titel seines Buches ist eher tiefstaplerisch zu verstehen, denn es werden neben Walen (Cetacea) und Robben (Pinnipedia) auch die Seekühe (Sirenia), sowie der Eisbär (*Ursus maritimus*), der Meerotter (*Enhydra lutris*) sowie der Küstenotter (*Lutra felina*, nach W. C. Wozencraft, 1993, korrekt: *Lontra felina*) behandelt. Dieses Buch ist eindeutig mehr als ein Bestimmungsbuch für den Säugetierliebhaber, da der Autor zusätzlich zu den Bestimmungshilfen Einführungen in die Biologie bietet. Er informiert über Schwimm- und Tauchvermögen, charakterisiert die Sinnesleistungen, behandelt ferner Probleme der Haltung und erwähnt auch die Rolle von Walen und Sirenen in der Mythologie. Die problembeladenen Beziehungen zwischen dem Menschen und den aquatischen Säugern werden ebenfalls erörtert, so wird der Einfluß von Meeressäugetieren auf die Fischerei besprochen und es wird auf Schutzprogramme und Beobachtungsmöglichkeiten hingewiesen. In den Abschnitten über die einzelnen Arten folgen auf eine Beschreibung der Art Bemerkungen zur Verbreitung, zur Bestimmung, zur Ernährung, Lebensweise und Fortpflanzung und Angaben zum heutigen Bestand. Die Verbreitung der einzelnen Arten wird durch klare, übersichtliche und informative Verbreitungskärtchen illustriert, die selbsterklärend sind. Das Buch gewinnt nicht nur an Informations-, sondern auch an ästhetischem Wert durch seine Illustrationen; die Habitusbilder der Wale sind durch die Graphikerin Marianne Golte-Bechtle zu Papier gebracht worden, die anderen behandelten Arten werden durch vorzügliche Farbphotos anschaulich gemacht. Gesteigert wird der positive Eindruck, welchen dieser Naturführer macht, durch seine sorgfältige drucktechnische Gestaltung. Ein Glossar bietet Erklärungen zu Fachbegriffen, eine Liste macht den Leser mit Institutionen, Zoologischen Gärten und Verbänden, welche sich mit dem Schutz aquatischer Säugetiere beschäftigen oder deren Biologie erforschen, bekannt. Ein kurzes Literaturverzeichnis und ein sechs Seiten langes Schlagwortregister schließen dieses erfreuliche Buch ab. Zwei Aussagen sollten korrigiert werden: Es ist nicht notwendig, für die Bartenwale neben dem gültigen Begriff „Mysticeti" auch das obsolete Wort „Mystacoceti" zu benutzen. Auf Seite 251 schreibt der Autor, daß die Geruchsorientierung über Geschmacksknospen auf der Zunge erfolge. Auch wenn Geruch und Geschmack eng miteinander verbunden sind, ist die Aussage so, wie sie im Text steht, vom Autor sicherlich nicht gemeint.

P. Langer, Gießen

Thiede, U.: **Auf Haustierspuren zu den Ursprüngen der Japaner. Vor- und frühgeschichtliche Haustierhaltung in Japan.** München: iudicium Verlag 1998. 152 pp., 55 Abb. ISBN 3-89129-429-8. DM 38,–

Der vorliegende schmale, aber inhaltsreiche Band der Zoologin und Japanologin U. Thiede befaßt sich mit Ergebnissen der japanischen Haustierforschung, die besonders in den 80er und 90er Jahren eine Fülle neuerer Erkenntnisse hervorgebracht hat. Das Ziel der auf breiter methodischer Grundlage (Morphologie, Biochemie, Genetik) durchgeführten japanischen Forschungsarbeiten war (und ist) darauf ausgerichtet, durch Vergleiche von alten japanischen Haustierrassen mit Haustieren des benachbarten asiatischen Festlandes Herkunft und Einwanderungswege der auf den japanischen Inseln auftauchenden Haustiere zu rekonstruieren. Damit eröffnet sich die Möglichkeit, die Geschichte der menschlichen Besiedlung Japans einer Klärung näher zu bringen, weil die Wanderwege der Haustiere mit jenen der sie haltenden Menschen zwangsläufig identisch sind. Sprachbarrieren ist es wohl zuzuschreiben, daß die Ergebnisse japanischer Haustierforschung in der westlichen Welt bis heute durchweg unbekannt geblieben sind. Das vorliegende, durch zahlreiche Verbreitungskarten und Dia-

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gramme reich illustrierte Buch, das auf eine Vielzahl japanischer haustierkundlicher wie auch anthropologischer Arbeiten zurückgreift, ist angetan, diese Lücke zu schließen. Auf zwei einleitende Abschnitte folgen 3. Forschungsgeschichte der Bevölkerungsentwicklung Japans (mit einer Darstellung zahlreicher Theorien), 4. Ergebnisse der neuesten anthropologischen Forschung in Japan, 5. Wegbegleitende Pflanzen und Haustiere, 6. Aktueller Stand der vergleichenden Haustierforschung in Japan, 7. Die Haustiere im einzelnen und 8. Von Mäusen, Menschen und Viren. Beschlossen wird der Band mit einer Zusammenfassung und Diskussion, die übersichtlich informiert, wann und von wo welche Haustiere den japanischen Archipel vermutlich besiedelten. Sieht man einmal von Schafen, Enten und Gänsen ab, kommen heute in Japan die gleichen sogenannten klassischen oder traditionellen Haustiere vor wie in Europa. Erwähnenswert ist allerdings, daß die Einwanderungen erst in den Jahrhunderten um Chr. Geburt oder noch viel später erfolgten, wo doch in Europa schon vor mehr als 6 000 Jahren Haustiere ein untrennbarer Bestandteil menschlichen Daseins waren. Das 224 Titel umfassende, vorwiegend japanische Arbeiten aufführende Schriftenverzeichnis unterstreicht, daß U. Thiede einen profunden Beitrag zur Haustierforschung in Japan vorgelegt hat, der nicht nur in jeder zoologisch-haustierkundlichen Fachbibliothek einen Platz beansprucht, sondern auch unter Prähistorikern, Anthropologen, Ethnologen und Kulturgeschichtlern Aufmerksamkeit verdient. Abschließend seien ein paar Randbemerkungen erlaubt. Bei der redaktionellen Überarbeitung des Textes ist übersehen worden, daß sich die Verbreitungskarte der Wachtel nicht in Abb. 52 (S. 132), sondern Abb. 53 befindet. Nicht einheitlich gehandhabt werden die lateinischen Haustiernamen, z. B. Equus przewalskii f. caballus, andererseits *Felis silvestris f. catus.* Und „rückverwildert“ sollte besser wohl „verwildert“ heißen. Schließlich ist auf S. 114 zu verbessern: „... 19% der untersuchten genetischen loci polimorph sind ....“. (nicht ist)

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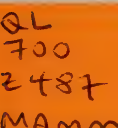
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DEUTSCHE GESELLSCHAFT FÜR SÄUGETIERKUNDE E.V. BERLIN

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Wissenschaftliche Kurzmitteilungen



ISSN 0044-3468 · Z. Säugetierkunde · 64(1999)6 · S. 321-384 · Dezember 1999

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URBAN & FISCHER

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
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Deutsche Gesellschaft für Säugetierkunde

Z. Säugetierkunde **64** (1999) 321–331

http://www.urbanfischer.de/journals/saeugetier

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Parturition, parental behaviour, and pup development in Indian false vampire bats, *Megaderma lyra*

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Receipt of Ms. 30. 03. 1999
Acceptance of Ms. 27. 08. 1999

Abstract

This report provides the first observations on parturition and postnatal development of free-ranging Indian false vampire bats. Pup sex ratio was balanced and pup forearm growth rates followed a logistic growth curve. Individuals showed considerable variance in the initial linear period of growth, ranging from 0.53 mm/d to 1.35 mm/d. Females started leaving pups behind ('park') either in the day roost or in special night roosts when pups were between 1 and 23 days old. Possible reasons for both the variability in growth and the onset of leaving pups on their own are discussed. Contact calls in this species consisted of repeated squeaking sounds and were not only emitted by mothers and pups, but also by other false vampires. They occurred most frequently in the morning and evening, during bursts of major activity in the colony.

Key words: *Megaderma lyra*, parturition, postnatal growth, night roosts, contact calls

Introduction

Parturition has been observed only in few bat species (Wimsatt 1960; Kunz et al. 1994), including one report on captive Indian false vampires (*Megaderma lyra*; Gopalakrishna et al. 1976). To our knowledge, this is the first description on parturition in free-ranging Indian false vampires.

Postnatal growth is an important life-history trait in mammals and represents an important index of maternal input (Oftedal and Gittleman 1989). Differences in this early development may affect fitness, such as offspring survival and future reproductive success (e.g. Clutton-Brock 1991; Hofer and East 1996). Growth is influenced by environmental variables such as food, temperature, maternal status, and condition. Young bats remain nutritionally dependent on their mothers for a prolonged period of time and female bats provide their young with milk until they achieve at least 90% of adult wing dimension and 70% of adult body mass (Kunz and Stern 1995). Hence, maternal input (Evans 1990) should play a crucial role in patterns of postnatal growth before pups achieve flight (Barclay 1994). We were interested to find out whether there are individual differences in postnatal growth and maternal attendance during early development of Indian false vampires.

0044-3468/99/64/06–321 $ 12.00/0

Materials and methods

Caves are natural roosts of Indian false vampires but this species exploits also man-made structures (Brosset 1962; Audet et al. 1991; Balasingh et al. 1994; Marimuthu et al. 1995). We investigated a temple-dwelling colony of about 60 false vampires in a small village about 15 km south-east of Tirunelveli (Southern India). Observations were conducted at the beginning of the dry season (February–May 1995), when females are expected to give birth and rear their young (Balasingh et al. 1994). Maximum outside temperature was 39.1 ± 2.6°C (mean ± sd; day, N = 38), minimum temperature was 25.9 ± 1.4 °C (night, N = 38). Average temperature inside the day roost was rather constant with 32.6 ± 0.9 °C during day (N = 43) and 31.2 ± 0.9 °C during night (N = 43).

The day roost was continuously illuminated with dim red light (nine 15 W bulbs), which did not seem to disturb the false vampires, as bats often hung close (<20 cm) to the bulbs. False vampires were caught with mistnets during emergence from the roost and removed from the net immediately. Lactating females carrying a pup were released without further handling to avoid injuries to the pup. Other individuals were sexed and weighed. Forearm length was measured to the nearest millimetre. Seventy percent of caught individuals carried a collar and coloured plastic beads from a previous study (Balasingh et al. 1992). The beads, however, were invisible in most of the cases and only a few bats could be identified from these tags. To improve individual identification we tagged 34 adults (~50% of the colony) with coloured wing bands (Museum Bonn, Germany, size E). Males were tagged on the left and females on the right forearm. "Parked" pups were tagged by painting either their claws with nail elamel or their ears with non-toxic dye (Marabu). When a pup was hanging alone at a roosting place we measured the right forearm with a pair of vernier callipers while standing on a chair beside the pup. We used the NONLIN function implemented in SYSTAT 5.0 (Wilkinson et al. 1992) to derive an equation for the forearm growth of pups. The equation was calculated combining data from 2 captive (colony in Munich, Germany) and 5 free-ranging false vampires of known age.

Total observation time in the day roost comprised 335 hours. Four other buildings in the vicinity of the temple, where false vampires perched during the night (night roosts) were observed during 105 hours. Night roosts were inspected daily to record whether any pup was 'parked' inside the roost. Observations in night roosts were done mainly with a night vision scope supported by stationary red-light torches.

Pup vocalisations were recorded with an electrostatic microphone (Petterson), amplified with an Ultrasonic Detector (Petterson D940), and stored into a Racal Store 4 DS tape recorder with a tape speed of 30 in/s. The recordings were digitised and analysed using a custom-made sound analysis software (Sona, M. Knipschild, Dortmund).

Statistical analyses were conducted with SYSTAT 5.0 (Wilkinson et al. 1992), following the procedures recommended by Sokal and Rohlf (1995) and Lamprecht (1992). The significance level was set as $\alpha = 0.05$ (two-tailed). Data are presented as mean ± SD or, when skewed, as median/interquartile range.

Results

Parturitions

Female false vampires gave birth to a single pup. The first pup was born on March 17th, the last one on April 18th. After this date no more pregnant females were observed. The total number of pups was about 20. Five females were observed during parturition and another female was seen eating the placenta immediately after parturition. All of these observations occurred between 11.05 h and 12.39 h local time, suggesting that the time around noon could be preferred for parturition (binomial test, $N = 6$, $x = 0$, $p < 0.05$).

During parturition females generally produced a hollow space between abdomen and wings by slightly spreading the wings around the abdomen. One female did not cover her abdomen and we were able to observe the emergence of the pup. At 11.05 h we saw the head and upper breast of the pup emerging out of the vagina. The mother bowed forward and licked the young, especially its head and flanks. At 11.08 h the pup emerged from the vagina. However, its left forearm still stuck to the vagina. The pup revolved round its

forearm and thus got into the position to clasp to its mother in carrying position. Its head was now close to the inguinal nipples and its legs close to the breast of its mother. At 11.16 h the mother stopped licking the pup. Twenty minutes later she started licking again, especially the pup's left flank. She repeatedly pushed her pup's left flank. At 11.38 h the pup's forearm suddenly emerged from the vagina, while the mother was still pushing the pup. The pup slipped slightly downwards and made a squeaking sound. It clasped the neck of the mother with its feet and the mother started to lick the pup's left forearm and, by pushing the pup to one side, her own belly intensively. At 11.45 h the placenta began to emerge, while the mother was still licking her belly. Then she slightly wrapped her wings around her pup. One minute later the mother again began to lick her belly and the pup. Now the placenta left the vagina completely and hung down the umbilical cord. At 11.51 h the mother started to feed on the placenta, which took her 4 minutes. Then she again licked the pup and her own genitals. At 12.05 h the mother wrapped her wings around the pup and rested.

After parturition all mothers licked their pup and their own genital region intensively, the latter may be a support to discharge the placenta. Mothers ate the placenta almost immediately after it had been discharged (N = 4, latency of feeding: 1.5/1–2 min, duration of feeding: 3.5/3–4 min).

False vampire pups cling to their mother in the 'carrying-position', venter to venter, the head pointing towards the anus of the mother. With its mouth the pup sucks at one of the two inguinal nipples. These nipples are special attaching warts, no functional teats. The pup wraps its legs around the neck of the mother, crossing them behind her shoulders. The wings are folded at the mother's flank.

When false vampire pups tried to get into this carrying position after birth their mothers assisted them in different ways. Two bats used their muzzles to guide their pups to teats and inguinal nipples. Two other bats made stretching movements while their pups tried to get into the carrying position after birth. Three different pups struggled 10, 20, and 45 minutes until they succeeded in reaching the carrying position. It seemed to be difficult and laborious for the pup, which is delivered head-first to revolve around itself and reach the carrying position. In the carrying position pups frequently lost the sucking grip to an inguinal nipple and the heads suddenly emerged out between the wings of the mothers. The mothers then pushed their pup back with their muzzle. Larger pups frequently hung pendant-like, grasping only the neck of their mother. In this position they stretched their wings, groomed themselves, and did wing flapping.

Sex ratio and growth rates

The sex ratio of identified pups was balanced (6 males and 6 females). The sex of two other pups was not determined. To derive a model for the forearm growth of false vampire pups we combined data of 5 pups (3 females, 2 sex unknown) of known age with data of 2 female pups from a captive colony in Munich. We computed a logistic equation (forearm length = 64.382 $\{e^{-0080(age+0.697)} + 1)^{-1}$) which appropriately fitted to the data (corrected $r^2 = 0.97$, Fig. 1). The mean birth forearm length calculated with this equation was 34 mm. During the first 22 days of development the slope of the logistic equation almost equalled the slope of a linear curve (Fig. 1). We took data from 6 individuals for which appropriate data were available for this period and calculated their individual growth rates. Individuals showed considerable variation, ranging from 0.53 mm/d to 1.35 mm/d (Fig. 2). Two pups parked in night roosts (Fig. 2, individuals no. 2 and 3) had relatively low growth rates, but the sample size does not allow a meaningful statistical comparison.

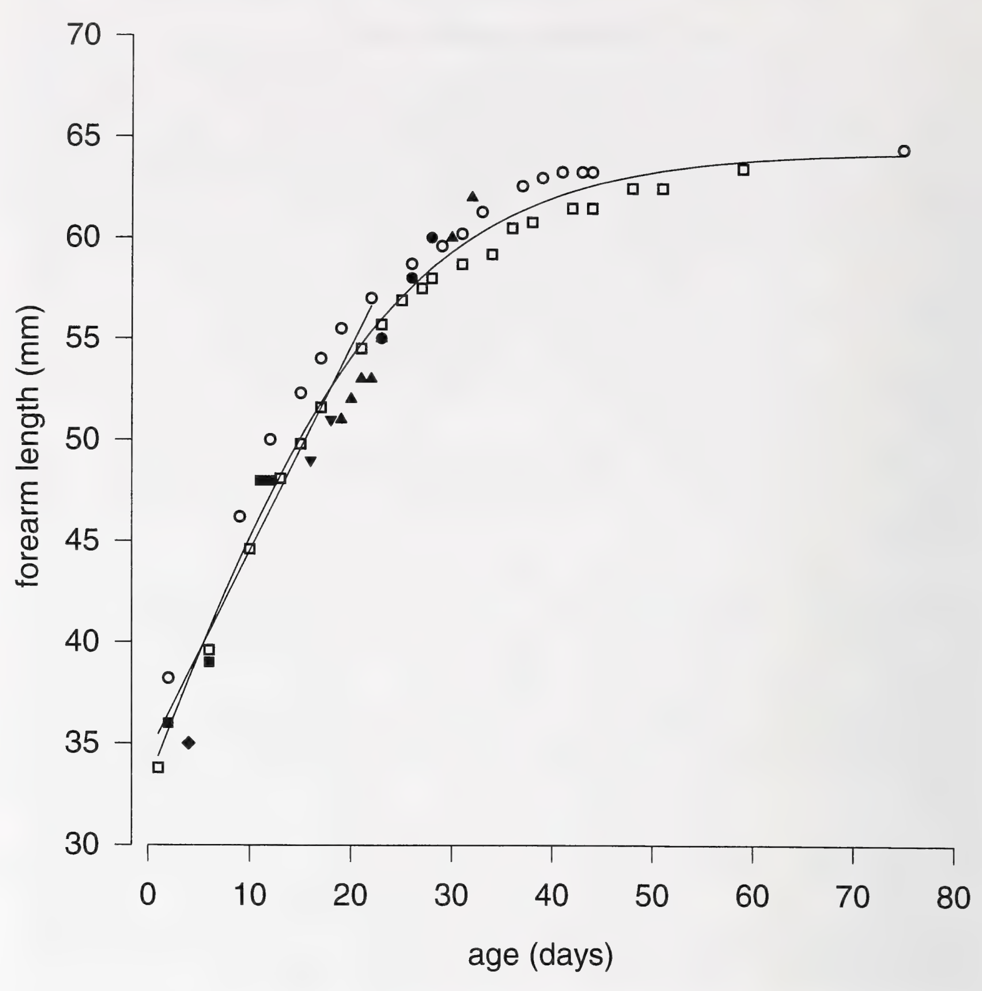


Fig. 1. Logistic growth model (forearm length = 64.382 $\{e^{-0.080(age+0.697)} + 1)^{-1}$), estimated using data of 2 captive (white symbols) and 5 free-ranging false vampires (black symbols). During days 1 to 22 growth almost follows a linear curve (forearm length = 1.008 age + 34.455).

'Parking' pups

Females carried their pups during flight even when the young had almost reached adult size (own observations; Brosset 1962). However, mothers also 'parked' their pup during night-time either in so-called night roosts (N = 4) or in the day roost (N = 4). Mothers leaving their pup in night roosts came to these roosts between 18.50 h and 19.10 h (N = 4), probably immediately after they had left the day roost. They chose a roosting place and started to 'park' their pup. This procedure was complicated and took some time. First mothers landed at the ceiling and hung with the pup in carrying position. Then they made rhythmic and jerky movements with their muzzles towards the pup's rump ('muzzle-pushing') and bowed themselves ventrally towards the ceiling, probably to give the pup the opportunity to grip the roost's surface with its legs. During these bowing movements mothers spread their forearms. They had to bow up to 12 times until the pup clung to the ceiling. This behaviour included several bouts of jerky muzzle-pushing and

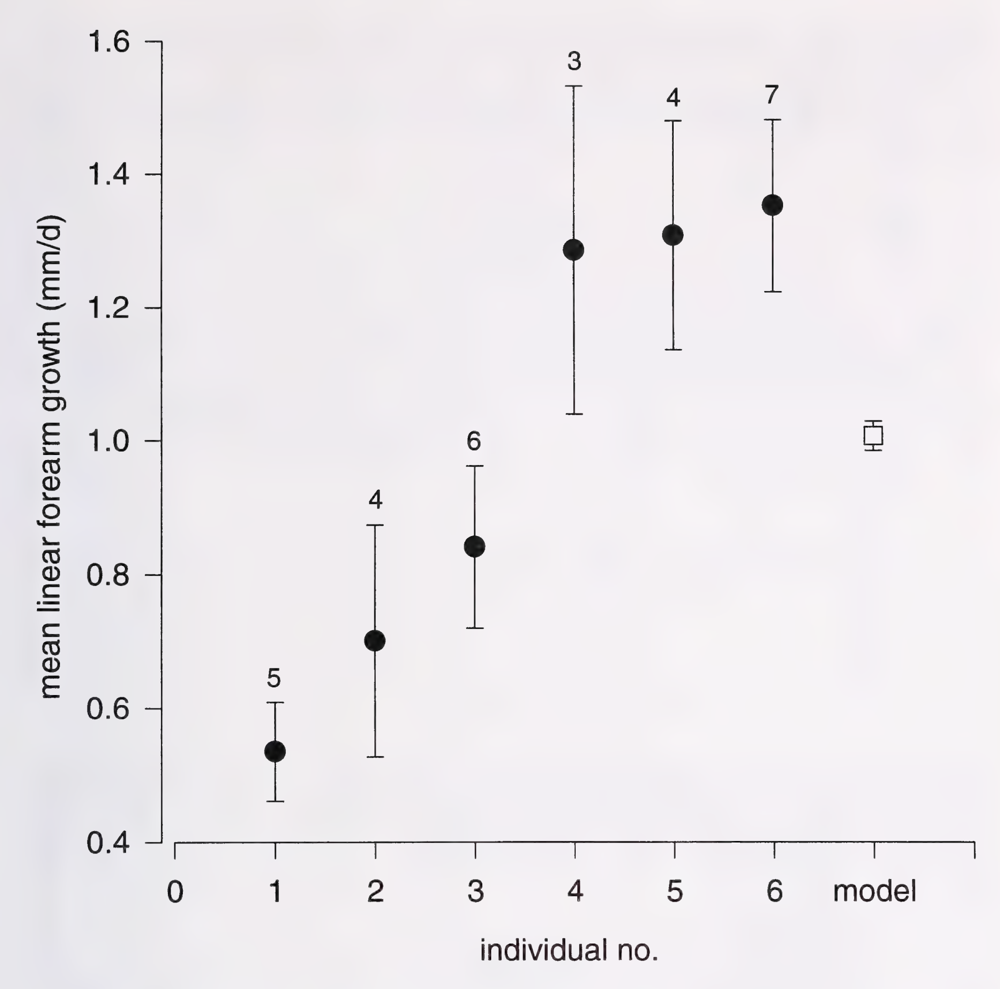


Fig. 2. Linear growth rates (±SD) of 6 individuals until day 22 compared with the linear proportion of the logistic growth curve from figure 1 (numbers refer to sample size on which the respective calculation is based).

bowing. The separation procedure lasted from 5 to 21 minutes (N = 4, median 9.75/8 –10.5 min). Immediately after the pup had attached to the ceiling the mothers left the roost. Pups were left alone for 23% of the time, whereas 77% of the remaining time the mother joined it and the two hung together (Tab. 1). Mothers stayed in a night roost at least a minute and maximum 202 min (N = 4) and pups were on their own for at least 3 and maximum 170 min (N = 4). Detailed data were available for one mother in night roost 2: her median attendance interval was 83.5/18.5–151.5 min (N = 12) and her median absence interval was 39.5/30–59 min (N = 10).

Age at 'parking'

At what age did mothers 'park' their pups? If exact pup age was not known (5 cases) we estimated the age using the logistic forearm growth model. For three pups the exact age was known. Age of pups 'parked' for the first time inside the temple varied from 2 to

Table 1. Time (in minutes) mothers spent at and apart from the roosting site of their young (NR = night roost)

place	total time	mother present	mother absent
NR 1	244	173 (71%)	71 (29%)
NR 2	2 196	1 682 (77%)	514 (23%)
NR 3	90	90 (100%)	0 (0%)
NR 4	129	104 (81%)	25 (19%)
total	2 659	2 049 (77%)	610 (23%)

Table 2. Forearm length (in mm) and age (in days) of pups when they were 'parked' for the first time (NR = night roost, DR = day roost, F = female pup, M = male pup, * = age calculated using logistic growth equation, see figure 1)

location	pup	forearm length (mm)	age (d)
NR 1	F5	51	11
NR 2	M3	45	10*
NR 3	M4	56	23*
NR 4	F1	–	16
DR	M2	35	2*
DR	F2	53	19*
DR	F3	52	17*
DR	F4	36	3

19 days, median age was 10.5/2.5–18 days (N = 4, Tab. 2). Pups 'parked' for the first time in night roosts were 10–23 days old, their median age was 13.5/10.5–19.5 days (N = 4, Tab. 2). However, the age difference of pups 'parked' in temple and night roosts was not significant (Mann-Whitney U-test, U = 10, p = 0.564).

First flight

Twenty-seven days after the first birth had occurred, the first pup was fluttering inside the temple. From then on the number of flying pups increased to at least 4 until the end of the study period. However, so far no pup seemed to leave the day roost. One pup made its first flight attempts when its forearm was 58 mm long.

Two days later its forearm length was 60 mm. This was the last time the pup could be measured, since its increasing flying ability made further measurements impossible. In contrast, another pup hanging in night roost 4 did not make any attempts to fly when its forearm was 62 mm long. A third pup in night roost 3 could be recorded until its forearm measured 58 mm. The two captive bats from the laboratory colony (Munich, Germany) started to fly when their forearms were 60.5 mm and 62.6 mm long. Their respective ages were 35 and 30 days.

Contact calls

Contact calls of false vampires consisted of repeated squeaking sounds with a peak frequency of about 12 kHz (Fig. 3). A total of 107 contact calls was counted between February 9th and April 14th (Fig. 4). Then contact calls occurred so frequently that we stopped

counting them. Interestingly contact calls could be heard from the very onset of the study and hence 54 of all recorded contact calls (50.5%) occurred before a single pup was born (Fig. 4). Contact calls were not equally distributed throughout the day. A comparison of total observation time between February 9th and April 14th and the frequency of contact

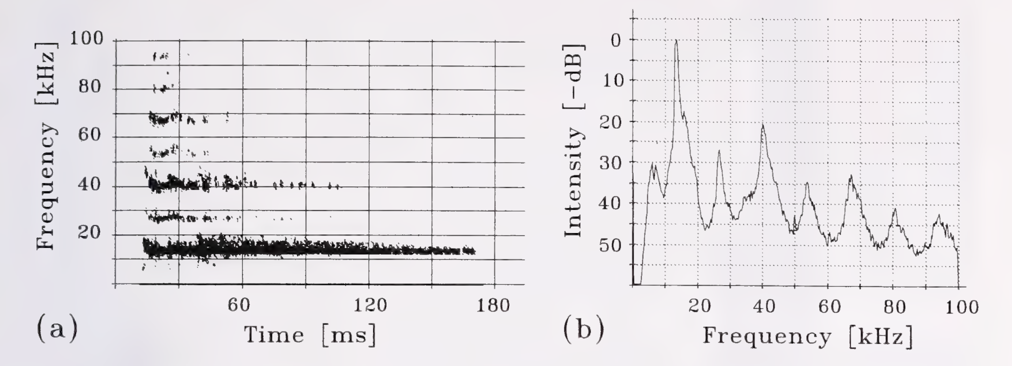


Fig. 3. Spectrogram (a) and sound spectrum (b) of a typical contact call of Indian false vampires.

Fig. 4. Cumulative numbers of contact calls (line) and pups (bars) during the study.

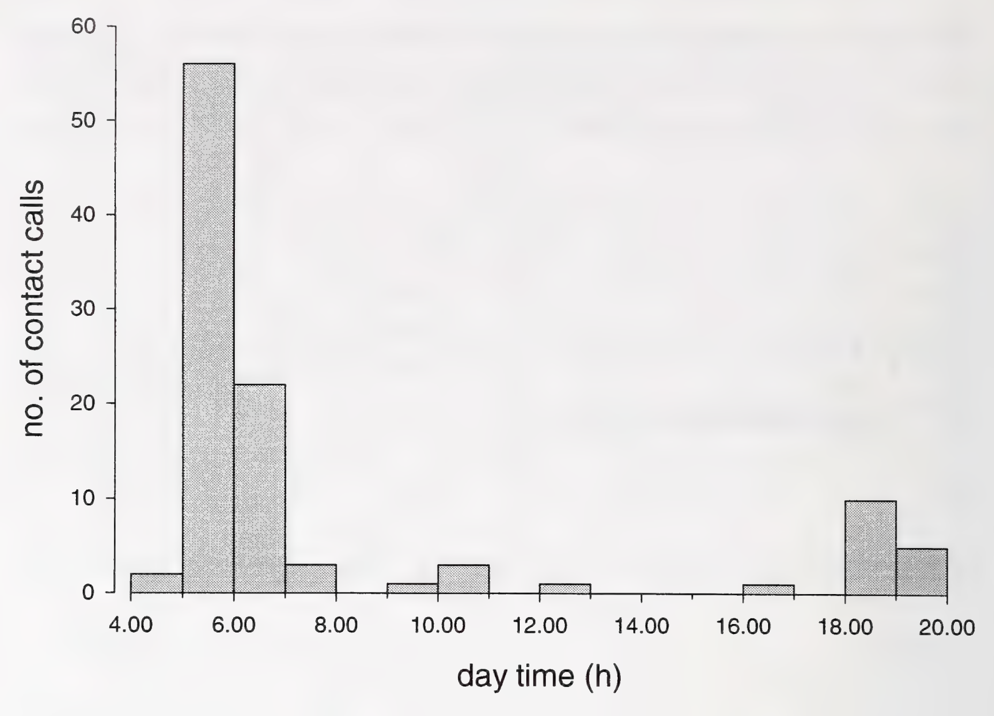


Fig. 5. Frequencies of contact calls at different times of the day.

calls revealed a significant difference (corrected Kolmogorov-Smirnov two-sample test, $N = 18$, $D = 0.444$, $p < 0.05$). The bats emitted contact calls more often in the morning during and after inflight (Fig. 5), when there were major movements in the colony.

Discussion

Parturitions

There are only few reports on parturitions in bats (WIMSATT 1960; KUNZ et al. 1994). Most microchiropterans appear to give birth by breech (feet first) presentation (KUNZ et al. 1994). Our observations support GOPALAKRISHNA et al.'s (1976) data that false vampires give birth head-first. Delivery by head first, however, may cause difficulties for the pup when trying to get into the carrying position, which is the same as already described for the closely related yellow-winged bat (*Lavia frons*; VAUGHAN and VAUGHAN 1987) and the African false vampire (*Cardioderma cor*; WICKLER and UHRIG 1969).

Births in 1995 occurred between March 17th and April 18th. Together with a study of BALASINGH et al. (1994) these data are in contrast with those of GOPALAKRISHNA and BADWAIK (1989), who suggested that parturitions of Indian false vampires throughout India occur within a narrow time window of 8–10 days in the second half of April. Also BROSSET (1962) suggested a strict periodicity of Indian false vampires in a colony in Aurangabad.

'Parking' and growth

This study supports the findings of HABERSETZER (1983) who states that false vampire mothers always leave their pups in the same place within the day roost.

There was considerable variation in the age and developmental stage at which females began to 'park' their pups. Larger young, which were 'parked' in the temple for the first time at an approximate age of 17–18 days, could have been 'parked' at other places before. However, as mothers 'parked' pups in night roosts for the first time at an age of 10–23 days, it is likely that pups were 'parked' for the first time in the day roost at a similar age. One pup found alone in the temple was probably not older than one day. The temple provided constant temperatures of more than 30°C during day and night, whereas temperatures in night roosts most likely were subject to higher temperature fluctuations. Before 10 days of age pups are almost naked and may have problems to thermoregulate. As temperatures in night roosts were lower than in the day roost there might be a higher age limit for 'parking' pups in night roosts compared to the day roost, possibly explaining the lower variance in detachment age in night roosts. Growth rates of 2 pups parked in night roosts were relatively low, but the sample size was too low to be conclusive.

The overall variability in the onset of 'parking' could stem from differential maternal foraging abilities or prey preferences. In captivity mothers do not attempt to catch large prey like mice, when carrying a pup (LEIPPERT pers. obs.). Hence, mothers might adapt the onset of 'parking' according to their foraging skills or prey preferences. On the other hand, mothers rely on the cooperation of their pup, which has to attach to the ceiling of the respective roost. Hence, the variability in onset of 'parking' could also be the result of different outcomes of a parent-offspring conflict (TRIVERS 1974).

Forearm growth rates showed considerable variation between pups. Growth rates and survival of pups may depend on maternal age, rank, and body size (CLUTTON-BROCK 1991; HOFER and EAST 1996), as well as on ecological factors such as prey abundance (e.g. HOFER and EAST 1996) or, especially important in bats, on temperature (TUTTLE and STEVENSON 1982). Currently there is no information whether a reduced growth rate has fitness consequences for false vampires.

Usage of night roosts

Why do mothers carry their pups to night roosts instead of leaving them in the day roost? We found pups with forearm lengths of more than 60 mm in night roosts. The transport of such large pups must be a considerable effort for their mothers. This expenditure could possibly be balanced by energy savings due to shorter distances to the foraging areas. However, the distance from the day roost to the observed night roosts did not exceed 200 m. Furthermore, mothers spent most of the time roosting with their pups. Thus, the energy savings for mothers may be negligible. Alternatively, if mothers forage close to the night roost pups may be safer, as their mothers would be within calling distance. There is, however, some evidence suggesting that at least the foraging area of one mother was rather far (~750 m) from the night roost where the pup was "parked" (AUDET et al. 1991). Mothers spent most of the night roosting time (77%) with their pups. We were not able to collect data for non-lactating females and do not know whether the resting time of mothers exceeded those of other false vampires. Thus, it is unclear whether this species spends generally little time foraging or whether mothers maximise their attendance time.

Contact calls

Infants of numerous bat species emit isolation calls which allow a mother to identify her pup (e. g. Fenton 1977; Gelfand and McCracken 1986; Thomson et al. 1985; Esser and Schmidt 1989; Scherrer and Wilkinson 1993). In the yellow-winged bat only mothers seem to call the pup (Wickler and Uhrig 1969). Because in Indian false vampires both mother and pup used the same type of sound to contact each other we consider the term 'contact calls' more appropriate than the term 'isolation calls'. Contact calls were most frequently emitted in the morning when mothers returned to the roost and looked for their pup. Often after exchanging several such squeakings the mother flew to the pup or both met, when the pup was already volant (Habersetzer 1983 and own observations). Since contact calls were also emitted before pups were born, it is likely that these calls do not only serve mother-pup recognition, but also other social purposes.

Acknowledgements

We thank Dr. J. Balasingh for providing his tagging data, and Gabi Leippert and Dr. G. Marimuthu for their helpful field assistance. Special thanks to Agnes Türk and Maike Pöttke for their professional logistic support. Rose Klein helped us in obtaining the relevant literature. Dr. Leonida Fusani gave helpful comments on earlier versions of the manuscript. We are indebted to Prof. Dr. Wolfgang Wickler from the Max-Planck-Institut für Verhaltensphysiologie, Seewiesen, and to Prof. Dr. Gerhard Neuweiler from the Universität München for funding the study.

Zusammenfassung

Geburt und Aspekte der Jungenaufzucht und -entwicklung bei Indischen Falschen Vampiren, Megaderma lyra

Dieser Bericht liefert die ersten Beobachtungsdaten zu Geburt und nachgeburtlicher Entwicklung von freilebenden Indischen Falschen Vampiren. Das Geschlechterverhältnis der Jungtiere war ausgeglichen und das Jungenwachstum, gemessen am Unterarm, folgte einer logistischen Wachstumskurve. Es zeigten sich jedoch große individuelle Unterschiede in der anfänglich linearen Wachstumsperiode (zwischen 0.53 mm/d und 1.35 mm/d). Als die Jungtiere zwischen 1 und 23 Tage alt waren, begannen Weibchen sie während der Ausflugperiode im Tagesquartier oder in speziellen Nachtquartieren zurückzulassen. Mögliche Gründe für die Wachstumsvarianzen und die unterschiedlichen Zeitpunkte, ab wann die Weibchen ihre Jungen allein ließen, werden diskutiert. Kontaktrufe von Falschen Vampiren bestanden aus wiederholten Quietschlauten und wurden nicht nur von Weibchen und deren Jungen, sondern auch von anderen Tieren produziert. Kontaktrufe im Tagesquartier traten am häufigsten morgens und abends auf, wenn die Tiere entweder einflogen oder sich auf den Ausflug vorbereiteten.

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Z. Säugetierkunde **64** (1999) 332–343

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Coats and moults of the water vole *Arvicola sapidus* Miller, 1908 (Rodentia, Arvicolinae) in southern Navarra (Spain)

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Receipt of Ms. 05. 01. 1999
Acceptance of Ms. 10. 08. 1999

Abstract

On the basis of 363 specimens captured in southern Navarra (Spain), the characteristics of the moults and coats of *Arvicola sapidus* were studied. The study of the moults was carried out on pigmentation present on the reverse side of the skins. The water vole has a first or juvenile coat which is less dense, shorter, and darker than later ones. After a certain period of time a juvenile moulting takes place, which is age-related, regular, and of a sublateral type. Most of the individuals that have gone through this moulting phase are immature (82 % ♂♂–93 % ♀♀). Following the juvenile moulting, the water vole acquires its second or subadult coat which, unlike the first coat, is lighter in colour and greater in hair density and length. In *A. sapidus*, the second or subadult moult takes place quickly and, like the first, is age-related and a sublateral type. Nevertheless, the second moulting phase is less regular. During the process of this moulting phase the specimens reach sexual maturity (78 % ♂♂–70 % ♀♀). This moult gives the water vole its third adult coat, which is longer and lighter. It forms one of the adult coats, which are indistinguishable except for winter coats. These are longer and thicker than summer coats. A series of seasonal adult moults takes/place without interruption after the adult coat has been acquired. The autumn moult is similar to the second or intermediate moult, which displays regular prints, at least in its first phase. The spring moult, which is less obvious, displays significantly irregular topographies. The development of the adult moult is also influenced by age and, in the case of the females, by the reproduction process.

Key words: *Arvicola sapidus*, coat, moult, Rodentia, Spain

Introduction

The information available on coats and moults of *A. sapidus* is scarce, which is not the case for other arvicolines. The first observations were made by Le Louarn and Saint-Girons (1977) and Gosálbez (1982) and more recently by Ventura and Gosálbez (1990). Others have concentrated almost exclusively on skin pigmentation in different subspecies (Miller 1912; Cabrera 1914; Rode and Didier 1946; Saint-Girons 1973; Reichstein 1982; Zabala 1983).

The aim of this study is to analyse and describe the moulting process of *A. sapidus* from southern Navarra, including coat characteristics, along with such relative factors as age, biometrics, sexual state, and seasons of the year.

Material and methods

363 specimens captured between 1983 and 1990 in southern Navarra (Spain) were analysed. The sample was divided into six classes of relative age (0–V), according to a series of morphological and bio-

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metrical characteristics: cranial and mandibular morphology, body weight, head and body length (HBL), condylo-basal length (CBL), and eye lens weight (EW) (Garde et al. 1993). The samples were classified according to the following sexual stages: immature, submature, and mature (Garde and Escala 1996 b).

In order to determine the stage of moult, the melanin prints on the inner surface of the skin were examined. The physiological development of the moult in *A. sapidus* was the same as described by Morel (1981) for *Arvicola terrestris* and followed the same model as observed in other rodents (España et al. 1985; Palomo and Vargas 1988).

As sexual differences were not observed in the coats and moults, the information obtained from males and females was evaluated jointly, excluding exceptions.

Results and discussion

First coat

This first coat is also known as the nest or juvenile coat (Morel 1981; Palomo and Vargas 1988). Two individuals were examined (Weight = 30.0–34.4 g; EW = 5.3–5.5 mg; HBL = 105–111 mm; CBL = 27.0–27.25 mm) in the final stages of acquiring the first coat. A fully pigmented surface in the specimens suggested a rapid acquisition of the first coat. This corroborates the observations made by Morel (1981) regarding *A. terrestris* and España et al. (1985) in *Mus spretus*, who concluded that these two species acquire their first coat at three weeks of age. Becker (1952) observed a similar time span in *Rattus norvegicus* and Palomo and Vargas (1988) in *M. spretus*. Stein (1960) observed in *Microtus arvalis* a time span of 14–21 days and Kahmann and Tiefenbacher (1970) in *Eliomys quercinus* 28–32 days. It was therefore extremely probable that the above-mentioned specimens of *A. sapidus* likewise displayed a fully developed first coat three weeks after birth.

Five specimens displaying a perfectly constituted coat and not lacking any melanin prints in the coat reverse (1.38 % of the total sample) were analysed. *A. sapidus* from southern Navarra has a distinctly coloured first coat: it is dark, almost black, with a dark grey ventral area and greyish-brown back and flanks. The hair of this first coat is the least thick and the shortest of all subsequent coats (Garde 1992).

Ventura and Gosálbez (1990) also observed the darkest colour in the first coat in *A. sapidus* from the Ebro River Delta, a characteristic common in most rodents: *A. terrestris* (Morel 1981; Ventura 1988), *Microtus chrotorrhinus* (Martin 1973), *M. spretus* (España et al. 1985).

The specimens studied with this coat presented biometrical data demonstrating a significant time span (Weight = 62.9 ± 13.2 g, n = 5; EW = 7.2 ± 0.8 mg, n = 4; HBL = 134.8 ± 9.1 mm, n = 5; CBL = 30.51 ± 1.57 mm, n = 5), which suggested that this coat is normally maintained for a certain period of time. Such a conclusion is supported by the observations made by Palomo and Vargas (1988) on *M. spretus*. These authors noted a period of 10–22 days from the acquisition of the first coat until the start of the first moult. The measurements of the two *A. sapidus* specimens with first coats which Ventura and Gosálbez (1990) studied are included in the data.

All the first-coat animals showed signs of sexual immaturity.

First moult

Thirty-one specimens (8.56 %) with melanin prints corresponding to the first moult were studied. All of them had a totally or partially developed first coat and, with one exception, displayed regular pigmentation marks.

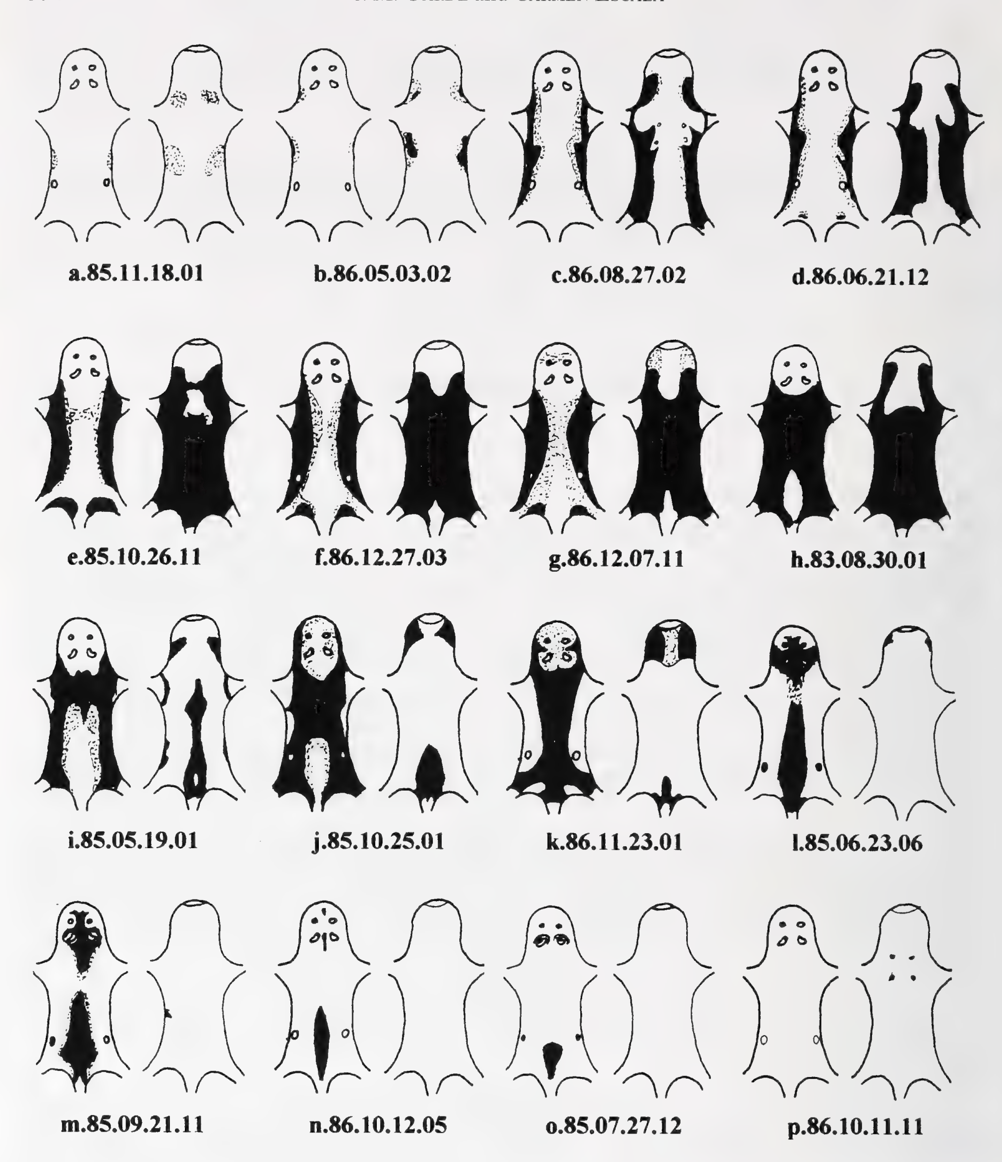


Fig. 1. Sequence of the first coat change in *A. sapidus* from southern Navarra. The silhouettes correspond to the inner surface of the skin. The black areas illustrate the accumulation of melanin and the spotted areas illustrate the low concentration of pigment.

This first change of coat in *A. sapidus* specimens from southern Navarra is a sublateral type and shows a regular topography, as was reported by Ventura and Gosálbez (1990). This is the most common model found in rodents: Saint-Girons (1967) and Sans-Coma et al. (1987) in *Apodemus sylvaticus*; Kahmann and Tiefenbacher (1970) in *E. quercinus*; Martin (1973) in *M. chrotorrhinus*; Morel (1981) in *A. terrestris*; España et al. (1985) in *M. spretus;* Sans-Coma et al. (1987) in *Rattus rattus.* However, the moulting process in the water vole shows certain unique features (Fig. 1: a–p). The pigment appears at four points simultaneously: two in the mid-ventral area and the other two near the neck. The pigment gradually progresses towards the flanks, then slowly to the back and much more rapidly

in the direction of the abdomen, finally reaching the pectoral and cephalic zones. The re-absorption of pigment starts at the central-ventral region and continues on, disappearing according to the pattern of its original appearance.

Certain minor variations in this general process have been observed, with one specimen displaying a completely atypical moult pattern. España et al. (1985) described similar cases in *M. spretus* attributing them to individual variations.

Table 1. Distribution of *A. sapidus* from southern Navarra according to age and moulting phase. "A. 1st coat": acquisition of the first coat.

Age	0	I	II	III	IV	V	Total
A.1st coat	2	–	–	–	–	–	2
1st coat	4	1	–	–	–	–	5
1st moult	2	24	5	–	–	–	31
1st phase	2	8	–	–	–	–	10
2nd phase	–	9	–	–	–	–	9
3rd phase	–	6	5	–	–	–	11
irregular	–	1	–	–	–	–	1
2nd coat	–	1	3	–	–	–	4
2nd moult	–	–	17	59	–	–	76
1st phase	–	–	6	2	–	–	8
2nd phase	–	–	11	21	–	–	32
3rd phase	–	–	–	19	–	–	19
irregular	–	–	–	17	–	–	17
3rd coat	–	–	–	–	29	27	56
3rd moult	–	–	–	–	109	80	189

Table 2. Values of *A. sapidus* from southern Navarra corresponding to the first moult (1st, 2nd, 3rd phase or irregular) or second coat. n: number of specimens; x: average; s: typical deviation; t: results from Student test on comparisons between successive phases; level of significance: ns = not significant; * = $p < 0.05$; ** = $p < 0.01$: *** = $p < 0.001$.

	Phase	n	x	s	Range	t
EW	irregular	1	9.7	–	–	–
	1st	9	9.0	0.7	7.8–10.3	4.88**
	2nd	9	10.5	0.6	10.0–11.6	2.58*
	3rd	10	11.4	0.9	10.5–13.3	2.47*
	2nd coat	3	13.1	1.2	12.1–14.9	–
WEIGHT	irregular	1	128.9	–	–	–
	1st	10	86.0	16.3	53.1–113.7	3.83*
	2nd	8	111.9	12.7	83.2–130.3	4.13***
	3rd	11	138.0	15.1	100.3–157.8	2.12 ns
	2nd coat	4	155.9	12.0	143.6–173.5	–
HBL	irregular	1	163	–	–	–
	1st	10	146.2	5.4	138–155	5.82***
	2nd	8	160.2	4.6	153–167	3.91**
	3rd	11	172.0	7.5	161–184	0.99 ns
	2nd coat	4	176.2	6.2	172–187	–
CBL	irregular	1	34.30	–	–	–
	1st	10	31.96	0.91	30.50–33.50	4.64***
	2nd	9	33.75	0.75	33.15–35.40	4.78***
	3rd	11	35.85	1.13	35.20–37.30	0.75 ns
	2nd coat	4	36.31	0.61	35.80–37.35	–

It was observed that the end of the first moult coincided with the start of the second change of coats in three specimens. This gave rise to overlapping moults, an event that has been observed in other rodents (Kahmann and Tiefenbacher 1970; Sans-Coma et al. 1987). The three specimens were captured between September and December, which could indicate that the proximity of winter speeds up the onset of the second moult.

Despite the reduced size of the sample, it is possible to establish a relationship between the sequence of the first moult and the relative age of the animals (Tab. 1). Taking into account the division of the ventral fringe of melanin and the division of the dorsal fringe, the process of the first moult is comprised of three phases: first (Fig. 1: a–h), second (Fig. 1: i–k), and third (Fig. 1: 1–p).

There is also a clear relationship between the duration of the moulting phases and growth, which shows statistically significant biometrical differences (Tab. 2). These values are similar to those given by Ventura and Gosálbez (1990) in specimens of water vole captured at the Ebro River Delta, which had undergone the first moult. It can be inferred that both the start as well as the process of the first moult depends entirely on the age of the animal, suggesting that it is genetically controlled (Sans-Coma et al. 1987 for *A. sylvaticus*).

In other species the first change of coat took place between the first 3–8 weeks of life, as in the case of *A. terrestris* (Morel 1981) and *M. arvalis* (Stein 1960), 4–8 weeks in *M. spretus* (España et al. 1985; Palomo and Vargas 1988) and *R. rattus* (Sans-Coma et al. 1987) or 6–11 weeks in *R. norvegicus* (Becker 1952) and *E. quercinus* (Kahmann and Tiefenbacher 1970).

Most of the specimens undergoing the first change of coat were immature (81 % male and 93 % female) (Garde and Escala 1996 b). The presence of mature specimens among first moulters has been mentioned by España et al. (1985) in *M. spretus*, Sans-Coma et al. (1987) in *A. sylvaticus* and Ventura (1988) in *A. terrestris*.

Given that in the first months of the year hardly any young animals are captured (Garde and Escala 1996 a) would seem to confirm the fact that the moulting process develops irrespective of the time of year. It can therefore be assumed that both the start and the progression of the first moult depend entirely on age.

Second coat

In four specimens, the second or subadult coat (Morel 1981) showed no signs of melanin prints. This leads to the assumption that this coat lasts only a short time as it is followed soon thereafter by a second moult. This observation has been confirmed by other authors: Kahmann and Tiefenbacher (1970) in *E. quercinus*, España et al. (1985) and Palomo and Vargas (1988) in *M. spretus*, Sans-Coma et al. (1987) in *R. rattus* and by Ventura (1988) in *A. terrestris*.

A thicker and lighter coloured coat differentiates the second coat *A. sapidus* from the juvenile one (Garde 1992). These characteristics have also been observed in other rodents such as *M. spretus* (España et al. 1985), *R. rattus* (Sans-Coma et al. 1987), *A. terrestris* (Ventura 1988). The prevailing colour in the ventral region is light-grey, unlike the dark grey colouring found in the first coat. This is due mainly to the fact that in this second coat the hair appears to be longer and lighter in colour. The prevailing colour of the hair in the flanks and the dorsal region is a greyish-brown.

The age (Tab. 1) and biometrics (Tab. 2) of the second-coat specimens were similar to those of the group in the process of completing the first moult. The only significant differences were detected in the EW, which confirmed the brief duration of the second coat. The four second-coat specimens consisted of one sexually mature male and 3 immature females.

Second moult

76 specimens with melanin prints corresponding to the second moult were analysed. The three specimens previously mentioned displaying an overlap of the first and second moult were not included. The second change of coat in *A. sapidus* from southern Navarra is sublateral and is similar in some aspects to the first one, although its development is rather irregular, as can be observed in figure 2 (a–l).

In addition to some variations described in the model, 17 specimens displayed totally irregular designs, with no apparent relationship to the moult sequences already described. However, these designs can be said to belong to the second moult, by reason of the age (class III) of the specimens as well as the fact that most of the designs show a slight resemblance to the second and third moult phases, typified by an overlaying, irregular distribution common for adults.

Several specimens displayed melanin prints corresponding to the third moult without having reached even the end of the second moult (Fig. 3: i–l). Most of the specimens with overlying designs were captured in autumn or at the beginning of winter.

The second moult, also known as the intermediate, postjuvenile or subadult moult was also observed in different species of rodents (Becker 1952; Stein 1960; Kahmann and Tiefenbacher 1970; Martin 1973; Morel 1981; España et al. 1985; Sans-Coma et al.

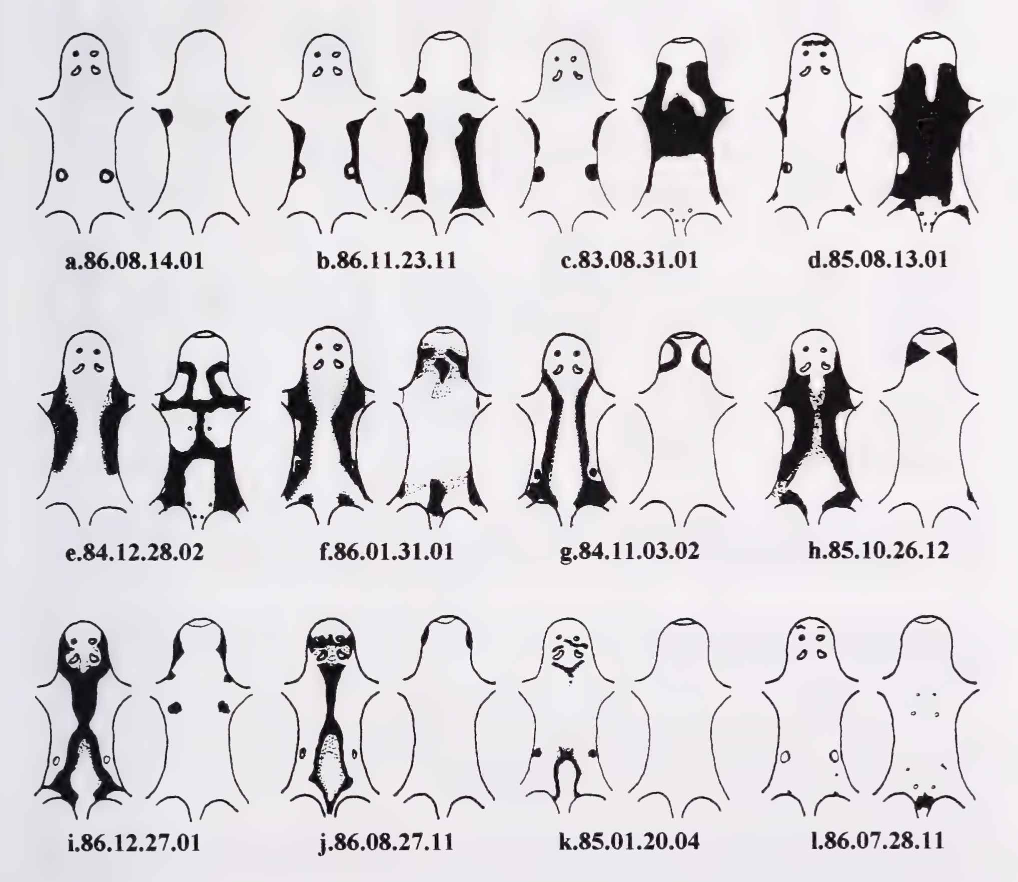


Fig. 2. Sequence of the second moult in *A. sapidus* from southern Navarra.

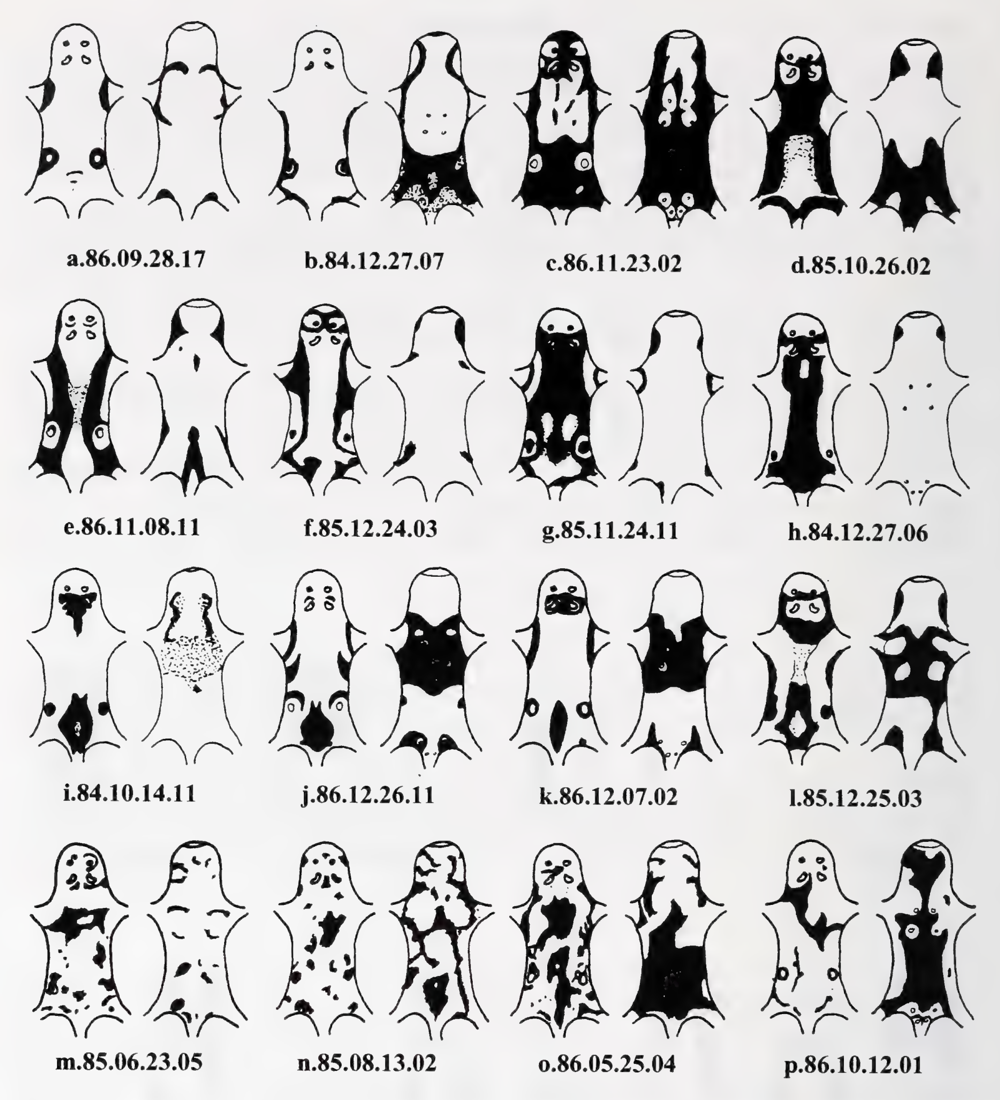


Fig. 3. Adult moults in *A. sapidus* from southern Navarra: sequence corresponding to the first phases of the seasonal moult (autumn moult) (a–h), specimens with the second moult overlying the third moult (i–l), displaying scattered melanin prints (m–n) and extensive pigmented marks (o–p).

1987; PALOMO and VARGAS 1988; VENTURA 1988). Moreover, the authors agree on the fact these specimens develop the second moult more irregularly than the first, with obvious individual variations.

In the second moult, as in the first, the split of pigment markings in the ventral region to the cephalic and caudal regions and the separation of the dorsal fringe divide the process into three phases: first (Fig. 2: a–e), second (Fig. 2: f–j) and third (Fig. 2: k–l). It was impossible to include those specimens that displayed irregular moults in any of the phases.

A clear relationship exists between the duration of the moulting phases, age (Tab. 1), and growth (Tab. 3). Furthermore, the biometric differences observed in the consecutive

Table 3. Values of *A. sapidus* from southern Navarra corresponding to the different phases of the second change of coat (1st, 2nd, 3rd and irregular). n: number of specimens; x: average; s: typical deviation; t: results from Student test on comparisons between successive phases; significance level: ns = not significant; * = p < 0.05; ** = p < 0.01; *** = p < 0.001.

Phase	n	x	s	Range	t	
EW	1st	6	13.8	1.6	11.9–15.9	2.78**
	2nd	27	16.2	1.9	11.9–18.9	2.92**
	3rd	14	17.9	1.5	14.6–20.5	
	irregular	9	17.6	1.8	15.4–20.8	
WEIGHT	1st	8	161.1	22.1	125.3–198.2	1.75 ns
	2nd	29	176.8	22.6	144.7–248.2	2.01*
	3rd	17	191.2	24.7	159.3–260.0	
	irregular	14	181.5	18.3	147.8–207.1	
HBL	1st	8	180.4	8.2	172–197	3.39**
	2nd	30	188.4	5.2	179–198	0.55 ns
	3rd	18	191.1	9.6	170–202	
	irregular	15	189.0	7.0	169–197	
CBL	1st	8	37.25	0.82	36.1–38.5	2.33*
	2nd	32	38.05	0.87	36.8–39.9	2.97**
	3rd	16	38.78	0.64	37.8–40.1	
	irregular	17	38.39	0.96	37.0–40.5	

moulting phases were statistically significant in most cases. This was also the case with the other parameters of the third phase of the first moult and the first phase of the second moult. Nevertheless, the differences between the second coat specimens and those still undergoing the first phase of the second moult were not quite as significant, which reinforces the hypothesis suggested earlier concerning the brief duration of the second coat.

Specimens with irregular moults displayed intermediate biometric values (Tab. 3) between the second and third phase of the moult and no significant differences were evident. These data support the aforementioned theory of a possible similarity between these designs and those typical for the phases.

Among those specimens undergoing the second moult, and captured from autumn to the beginning of winter, 22 % of the males and 30 % of the females were immature. This attests to the delay of the onset of sexual maturity for animals born at the end of the reproductive period (Garde and Escala 1996 b).

A. sapidus from southern Navarra reaches sexual maturity mainly during the second moult, like the water vole from the Ebro River Delta (Ventura and Gosálbez 1990) and several other species of rodents (Morel 1981; España et al. 1985; Sans-Coma et al. 1987).

Most of the animals which were in the process of a second moult were captured between the end of the summer or in mid-winter, coinciding with the capture of those animals from classes II and III (Garde and Escala 1996 a). Hence one might believe that the second moult also is mainly determined by age.

Adult coats

Once the second moult has finished, the animals acquire a third coat which is the first adult coat. Later on the specimens will go through a series of moults, influenced by environmental conditions, sex and age, which will lead to the acquisition of the adult coats.

56 specimens (22.8 % of the adults), with totally formed adult coats and without melanin prints, were studied. This small amount suggests that little time elapses between the two consecutive moults. Although it was not possible to distinguish between the adult coats themselves, two types of coats associated with the seasons were differentiated; one in the winter, which is thick and made up of much longer hair, and one in the summer. Such observations have been made by Ventura and Gosálbez (1990) in *A. sapidus* from the Ebro River Delta.

The pigmentation of the adult coat is lighter than that of the second coat, a characteristic which becomes more noticeable with age. In some older individuals, yellowish markings are displayed which vary from one individual to another (Garde 1992).

The 56 sample specimens all belonged to age classes IV and V (Tab. 1), which confirms the existence of several coats following the first adult coat. All the specimens with third or later coats, with no evident signs of moult were sexually mature, except for two males corresponding to age class IV, captured in February and in December (Garde and Escala 1996 b). The disproportion that existed between the males (16 specimens–11.6 % of the adult males) and the females (40 specimens–37.4 % of the adult females) was striking. These data suggest that the onset of a new moult in females might be influenced by physiological processes connected with reproduction.

The distribution of adult specimens with the third coat throughout the year reaches a maximum in March (35 %) and in September (36 %). These months coincide with the end of winter and summer and are periods with lowest moulting activity. However, it is likely that this monthly sequence is also influenced by the sexual activity of the female as previously mentioned.

Adult moults

In the analysed sample of the 245 specimens with totally formed adult coats, 189 (77.2 %) showed signs of moulting. All were sexually active, except 9 (6 males and 3 females), and were captured between November and February (Garde and Escala 1996 b).

Moulting adult specimens could be found every month of the year (64–87 %). The monthly frequencies of moult were higher between October and January and lower in February and March. The higher frequencies seem to correspond to a possible autum moult. The increase in percentage of moult beginning in April could be due to the commencement of spring moult and to the beginning of mating activity (Garde and Escala 1996 b).

The identification of two coat types in the adult specimens, one in winter and one in summer, suggests an autumn and spring moult. These two moults allow the animals to acquire the above-mentioned coats. Some authors (Saint-Girons 1967; Morel 1981) refer to such changes in adult coats as "seasonal moults", owing to their relationship with the environment.

Other authors, e. g. España et al. (1985) for *M. spretus* and Sans-Coma et al. (1987) for *R. rattus* insist on there being no relationship between the changes of the adult coat and the time of year; both cases were observed in southern Spain.

Only 20 % of the specimens (20 males and 18 females) showed uniform designs. The majority (28) was captured between September and January and all belonged to age class IV, which suggests that the first adult moults maintain a certain uniformity but, show variations with time.

This group of young adults displaying a regular moult undoubtedly corresponded to samples that had just reached adult age at that time of the year and were going through the autumn moult. In fact, several animals that were going through the third phase of the second moult displayed overlying melanin prints typical for the third moult (Fig. 3: i–l), and thus corresponded to the autumn moult. As has already been stated, this moult nor-

mally takes place between September and January. Most of its sequence was established (Fig. 3: a–h), except for the final phases, either due to the lack of specimens displaying those markings or because the final reabsorption of pigment was irregular. The autumn moult started from the lateral glands. The remainder of the process was very similar to the subadult moult (Fig. 2), although its development was somewhat more variable and irregular. The characteristics of the autumn moult for *A. sapidus* coincide with MOREL's (1981) observations in *A. terrestris*.

It was impossible to determine the sequence of the spring moult since all the specimens captured during this season displayed irregular topographies. It is therefore probable that its development is more irregular, unlike the autumn moult, as noted by VENTURA (1988) for *A. terrestris*.

The majority (80 %; n = 151) of specimens with adult moults displayed irregular markings. Nevertheless, it should be pointed out that in several specimens there was a variation in pigmentation as well as in the way the hairs were renewed in the lateral gland region. This fact, which was observed by QUAY (1968), has also been confirmed by VENTURA and GOSÁLBEZ (1990) in *A. sapidus* from the Ebro River Delta. In some females a similar variation was also observed near the mammary glands (Fig. 3: c, p), which also was mentioned by VENTURA (1988) in *A. terrestris*.

The appearance of small melanin prints distributed as a mosaic pattern over the whole reverse coat (Fig. 3: m–n) was also observed in specimens from age class V. These "scattered" designs are a clear sign of the absolute irregularity that characterises coat changes in older individuals and observed by MOREL (1981) in *A. terrestris*.

The existence of irregular designs of large melanin spots (Fig. 3: o–p) was also recorded. This widespread pigmentation is a sign of a fast moulting process. 21 specimens, 3 males and 18 females (12 of which were in gestation) displayed these characteristics. Most of the specimens (12) which displayed this design, did so between May and August, the months of greatest sexual activity. If the female sexual activity was an influencing-factor in the onset of a new moult, these results now seem to strengthen the idea that sexual activity also affects the adult moulting process in *A. sapidus* from southern Navarra.

These observations coincide with those made by MOREL (1981) in *A. terrestris*, who pointed out that during the reproductive period the females in gestation displayed significant delays in their moults, which were later completed at the end of the gestation period or slowed down and took place between two pregnancies. This was noticed by the appearance of simultaneous hair growth. Similar effects have been found in other rodents, for example, in *A. sylvaticus* (SAINT GIRONS 1967).

Zusammenfassung

Felle und Fellwechsel bei Arvicola sapidus Miller, 1908 (Rodentia, Arvicolinae), aus dem Süden von Navarra (Spanien)

Es werden Angaben zu den Besonderheiten von Fell- und Haarwechsel einer Population von *Arvicola sapidus* (n = 363) aus dem Süden von Navarra gemacht. Die Untersuchungen beziehen sich auf Pigmentierungsflecke der Hautinnenseite. Die südwesteuropäische Schermaus zeigt ein 1. oder jugendliches Haarkleid, das weniger dicht, kürzer und dunkler ist als die folgenden. Danach erfährt sie einen 1. oder juvenilen Haarwechsel, der in Zusammenhang mit dem Alter steht; er ist sehr regelmäßig und vom sublateralen Typ. Der größte Teil von in diesem Haarwechsel befindlichen Tieren ist sexuell unreif (82–93 %).

Danach bekommt die Schermaus ihr 2. oder subadultes Haarkleid, das dichter, länger und heller als das vorangehende ist. *A. sapidus* beginnt bald mit ihrem 2. oder subadulten Haarwechsel, der mit dem Alter korreliert und von sublateralem Typ ist. Im Unterschied zum 1. Haarwechsel verläuft er unregelmäßiger. Während des Haarwechsels erreichen die Tiere allmählich ihre sexuelle Reife (78–70 %).

Der subadulte Haarwechsel führt zum 3. Haarkleid, das länger und heller als das 2. Haarkleid ist. Diesem 3. Haarkleid entspricht die Gesamtheit der adulten Haarkleider, die ununterscheidbar sind; das Winterfell ist von größerer Länge und Haardichte als das Sommerfell.

Nach der Bildung des adulten Haarkleids unterliegen die Tiere ständig einer Reihe von saisonalen Haarwechseln: Herbstlicher Haarwechsel, der ähnlich wie der subadulte Haarwechsel verläuft und auch eine gewisse Regelmäßigkeit zeigt, zumindest in den ersten Stufen, und der etwas weniger ausgeprägte Frühlingshaarwechsel, der Topographien von auffallend hoher Unregelmäßigkeit zeigt. Der Verlauf des Haarwechsels der adulten Tiere wird auch durch das Alter beeinflußt und im Falle der Weibchen durch die Fortpflanzungsprozesse.

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Z. Säugetierkunde **64** (1999) 344–355

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

The social organization of the Mandarine vole, *Lasiopodomys mandarinus*, during the reproductive period

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Receipt of Ms. 20. 04. 1999
Acceptance of Ms. 14. 07. 1999

Abstract

The social system in a free-living population of the mandarine vole *Lasiopodomys mandarinus* was examined in Selenginski District, Buryatia, by use of the mark-capture method. Mandarine voles lived in extended family groups. The members of the group occupied a common burrow and were strongly attached to it. The summer groups consisted of one breeding male,1–5 breeding females, and young of 1–3 generations with a mean of 8.7 (range 3–22) individuals per burrow. Most of the offspring remained within the natal territory at least up to 50 days. None of the 72 young males and only three of the 73 young females became reproductive while staying in natal burrows. The change of sire appears to be the necessary condition for the reproductive activation of philopatric daughters.

Thus, *L. mandarinus* exhibits a high level of sociality based on communal breeding, prolonged pair-bonding and parent-young relationships. This set of traits is also reported in the literature for *Lasiopodomys brandti*. It is suggested that sociality was characteristic of ancestral above ground form and represented the precondition to occupy the recent niche of the fossorial stenophage.

Key words: *Lasiopodomys mandarinus*, mating system, philopatry, territoriality, subterranean rodents

Introduction

The mandarine vole *Lasiopodomys mandarinus* inhabits the grasslands of China, Korea, North Mongolia, and the borderland in the south of the Transbaical region of Russia. Very little is known about its habits. Meanwhile, scanty information from the works of former authors (Fetissov 1955; Hyan-Van-Di 1960) and especially the recent studies in the Mongolia and Transbaical region (Dmitriev 1980; Smorkatcheva et al. 1990) characterise *Lasiopodomys mandarinus* as an extremely interesting aberrant form.

Apparently, throughout its range *L. mandarinus* leads an almost completely subterranean existence. Its burrows are extensive: the number of entrances is up to 50–70 and the tunnels are up to 95 m long. Most of the tunnels are close to the surface and serve to forage underground for roots and tubers. In Mongolia and Buryatia the mandarine vole feeds almost entirely on *Stellera chamaejasme* using both its massive roots and green parts (Dmitriev 1980; Smorkatcheva et al. 1990). Even when foraging for stems and leaves of *Stellera*, voles rarely go away more than 0.5–1 m from a burrow entrance which usually is near this plant (Smorkatcheva et al. 1990).

The reproductive period lasts in the Transbaical region at least from early April through late August. Winter breeding is likely although there is an autumn break (Smorkatcheva et al. 1990; Smorkatcheva 1993). Unlike most voles of grasslands – e. g. *Lasio-*

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podomys brandti, Microtus socialis, M. arvalis, M. gregalis, M. ochrogaster (SVIRIDENKO 1934; KHRUSTZELEVSKI 1954 b; TAITT and KREBS 1985; GETZ et al. 1987) – *L. mandarinus* does not display great outbreaks of numbers. Although it seems to undergo cyclic density fluctuations, their amplitude is comparatively low and the species is never very abundant. Even in optimal habitats the maximal density of burrows does not exceed 5–7 per hectare (DMITRIEV 1980). The reproductive potential of the mandarine vole is low compared with most other microtines. Mean litter size determined by the number of scars in the uterus was 3.65 (DMITRIEV 1980); the number of embryos in nature averaged 4.4; mean number of newborn in the laboratory was 3.3 (ZORENKO et al. 1994). Gestation is 22–24 days. Pups open their eyes only after 13–16 days and wean around 18–22 days. Females become sexually mature at about 38–45 days, males at 55–60 days (ZORENKO et al. 1994). Thus, this species demonstrates the set of characters associated with K-selection (MC ARTHUR and WILSON 1967).

Some data on the spatial organisation and group composition obtained during two field seasons were briefly reported earlier (SMORKATCHEVA et al. 1990). The aim of this study is to summarise the information on the mandarine vole social system based on data collected throughout 1986–1993.

Material and methods

Study area

This work was carried out in Selenginski District of Buryatia near Lake Torm, 16 km SWW Selenduma (50°53′N, 106°01′E).

Data are presented for the periods June–July 1986; August–mid September 1990; mid April–late May 1991; June–July 1992, and early August–early September 1993. Additionally, some information on spacing and burrow dynamics was obtained in late September 1986 and in late July 1990. At the beginning of each trapping period one of four areas (8–16 ha) within the gentle slopes was selected. We had to change trapping areas because of asynchronous decreases in number of different local populations separated by steep rocky slopes or agricultural fields. When the density of inhabited burrows was low (0.1–0.2 per ha), it was practically impossible to obtain sufficient amount of data. Thus, the local population with the highest density of burrows was selected. Microrelief and vegetation of these four areas are similar. The steppe community is dominated by *Festuca lenensis* with dispersed *Stellera chamaejasme, Artemisia frigida, Potentilla acaulis, P. tanacetifolia, Leontopodium* sp., *Thymus serpillum, Arenaria capillaris, Lilium tenuifolium, Youngia tenuifolia, Veronica incana, Rumex acetosella, Astragalus* sp., *Oxytropys* sp., etc. Everywhere more or lesser overgrazing results in vegetation impoverishment combined with increase of *Stellera chamaejasme* productivity (GORSHKOVA et al. 1977). In the areas under study its density varied from about 50 up to 150–200 individuals per 100 m^2.

Field studies

All burrows within the chosen area were marked by stakes. Thereafter, the area was inspected daily (early in the morning or after rain) to reveal fresh mounds and plugs of soil. Every fresh mound was plotted (1:75 or 1:150). In this way the data on dynamics for at least 30 days were obtained for 29 burrows. In addition, four burrows were monitored from the very first mounds and were plotted and measured at different stages of development. All burrows in the area were live-trapped. The traps were slightly buried at the fresh mounded burrow entrances, from two to ten per one burrow and were moved according to the movements of the fresh mounds. Slices of stale bread with sunflower oil were used as bait. The live-traps were checked at 3–4 h intervals from 6 a. m. to 11 p. m. We closed traps during very cold nights in autumn and in spring and during very hot afternoons in summer. When first captured, animals were marked by toe-clippings. At each capture voles were weighed, sexed, notes were taken on molt and sexual condition (vaginal smears were taken in females with open vulva). Most of the animals were released immediately. In the case of death of voles in live-traps they were autopsied in order to obtain additional information on the reproductive organs.

Data analysis

Those voles that weighed more than 26 g and/or had adult fur were classified as adults, the remainder as young. Scrotal males and pregnant, nursing, or perforate females were classified as reproductive, the others considered to be nonreproductive. The age of young was determined by the moult development and weight.

Since the composition of groups did not change significantly through a trapping period, our estimations of group size refer to a given session as a whole. Individuals that were not caught repeatedly were assumed to be residents of those group burrows where they were marked. In doing so it was recognised that for some animals (especially subadult individuals) this assumption is not true, and therefore the values of group size must be somewhat overestimated. When no unmarked voles were caught in a burrow for at least 10 days, it was presumed all residents older than 20 days to be marked and these burrows were considered as completely trapped. To verify this, 4 burrows were excavated at the end of the trapping session; of 9 animals caught by hand when excavating, 8 were marked. During spring (1991) and summer (1986 and 1992) sessions, most of the monitored burrows (22/27) were completely trapped. During fall sessions all members of a family apparently were not marked in any of 16 live-trapped burrows, because after the vegetation of *Stellera* had finished, the trapability of mandarine voles decreased.

Group territory sizes were determined on the basis of fresh mound plotting (25–48 points were obtained for each burrow) for a period of approximately one month.

Demographic background

At live-trapped areas the number of inhabited burrows per ha ranged from 0.7 up to 3.0, i. e. middle-high density in this species. Only during the spring session 1991, a low density (0.2 burrows per ha) population was under study. The mean number of adult females per adult male varied from 1 up to 5, with a mean value being 1.9. The sex ratio among young was near 1 : 1.

Results

As judged from the trapping data, mandarine voles live in extended family groups. The members of a group occupy the common burrow and are strongly attached to it. Of the 194 marked and repeatedly caught voles 92 % were caught at only one burrow.

Among adults marked throughout the first week of each trapping session, 72 % of males (13 of 18) and 64 % of females (19 of 28) were caught in the same burrow system up to the end of the given session.

Mating system

Of five burrows live-trapped during the spring session of April–May 1991 (the beginning of the reproductive period) three were inhabited by pairs of adults without offspring, one by one female with two young, and one by a single adult male.

At the onset of the reproductive period both polygynous and monogamous groups were present in the population. Of a total of 17 groups completely caught during the summer sessions, 7 (41 %) contained one breeding female, 7 (41 %) contained two breeding females, 2 (12 %) contained four and 1 (6 %) contained five breeding females. The number of breeding females averaged 2.4 (n = 9) in 1986 and 1.8 (n = 8) in 1992. Each of two excavated burrows inhabited by several reproductive females had only one large nest. Thus, there is evidence of joint rearing of pups. From pooled data of 1986 and 1992, reproductive males were present in 17 burrows of 21 live-trapped and in 15 groups of 17 completely caught. In five burrows "additional" reproductive males were observed. In one case the female changed her mate after the former had died. In three burrows the "additional" males were caught only once and, apparently, were dispersers. Only in one

case two adult males were present in the same burrow simultaneously for at least five days.

Of 16 burrows live-trapped during the autumn sessions (pooled data for 1990 and 1993), in 2, 11, and 3 burrows two, one and no reproductive females were present, respectively. In 5 burrows one adult scrotal male was caught, 8 units did not contain scrotal males. Each of the remaining three groups included two scrotal males, one of which being an adult overwintered individual, and another being a young of this year.

Parent-young relationships and natal dispersal

During the spring trapping period only two young males were caught born approximately at the end of March; in mid-May they lived in the natal burrow with an adult female, apparently their mother.

Already in June two cohorts of young were live-trapped in some of the burrows: individuals born in late April–early May and those born in mid-late May. Simultaneously the newborn pups may be present in nests, as was shown by the subsequent trapping. Of a total of 14 family groups completely trapped by July where young were present, 3 included at least three litters, 9 at least two litters and one at least one litter. For these groups, the mean number of the young known to be present was the same in 1986 and 1992 and consisted of 6.4 individuals.

In August–September the young from the same group usually belonged to the same cohort born in July; the older young voles were caught in only three burrows of 16 live-trapped.

The majority of juveniles marked during the first week of each trapping period at 20–30 days of age were recorded staying at the natal site up to 50–60 days, and some of them even up to 70–80 days (Fig. 1).

All young males (n = 72) and most young females (70 of 73) remained nonreproductive while staying in their natal burrows. In late June–mid July 1992 three cases of reproductive activation in young philopatric females were registered: a pregnancy in a female

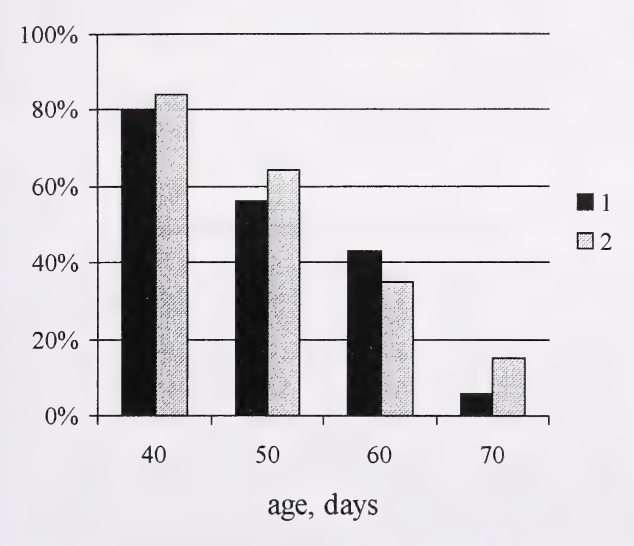


Fig. 1. Proportions of marked juvenile mandarine voles known to remain at natal territory up to the ages of 40, 50, 60, and 70 days. 1-males (n = 30), 2-females (n = 22).

of about 60 days and the phase of late proestrous-estrous in two females of about 40 days. It is noteworthy that one of the estrous females and the pregnant female were from the same family group, where an old mature female (their mother?) was present and the change of the sire-male occurred.

The composition of groups at the onset of the reproductive period allows to suppose dispersion of young males to be obligatory. Five males marked within natal territories were then captured outside at distances of 20–80 m. Two of them were found in the territories of the adjacent groups, the others at single burrow entrances. They were at an age of 45–75 days when dispersing; all but one were registered as nonscrotal. None of them were caught later. The rather long distance of natal dispersal is likely in these cases because all burrows within a radius of at least 100 m were live-trapped. Besides, 7 unmarked males at the age of 40–60 days were caught (each only once) near single burrow entrances, outside permanent family burrows. These individuals also seem to be dispersers. Two to three voles of the same age were captured at the same entrance, suggesting that they could be littermates.

Concerning the young females, two facts of their resettling in the adjacent burrows (distances 40 and 45 m) were recorded. These individuals were at least 70 days old when dispersing. Both were caught at the new sites as reproductive. Besides, five young females were initially marked in small recent underdeveloped burrows and were most likely among the founders of new breeding units.

All dispersers except one male and one female were registered in late June–mid July.

Size of groups

In spring, at the very beginning of the mass breeding period, all families were small and included 2–3 individuals.

According to the data of 1986 and 1992 for completely trapped burrows, in June–July the average social group contained 9.4 (n = 9) and 8.0 (n = 8) individuals, respectively. By July 1986 the number in one of the families reached 22 individuals; afterwards this family and group burrow gradually divided into two. The former mature male remained in one part, the new unrelated male appeared in another. The formation of new families was observed in early July 1986 (2 groups) and mid-July 1992 (1 group). From the very beginning, each of them consisted of one male with two females. Among the founders were both young and adult individuals.

During the late summer-fall the mean number of individuals caught per burrow was 3.47 and 3.72 in 1990 and 1993, respectively.

Spacing and territorial relationships

In *L. mandarinus* the density of inhabited burrows is comparatively low; the nearest ones usually are separated by a distance of several dozens of meters. Although this space is often holed by the set of destroyed or left tunnels, it seems to prevent a direct contact between the resident individuals from distant groups. Occasionally burrow-clusters were observed, several group territories being located close to each other (Fig. 2). In such cases burrow systems of different family groups were not connected by tunnels. Members of a certain group normally did not visit strange burrows. During 5 trapping sessions only 9 marked voles were observed to intrude. Among them, 4 individuals (2 young males and 2 young females) most likely were dispersers. Three.voles (one adult female and two adult males) lost their mates and were probably looking for new ones. The remaining two voles were a pair occupying an adjacent burrow, of which hosts had disappeared two weeks before.

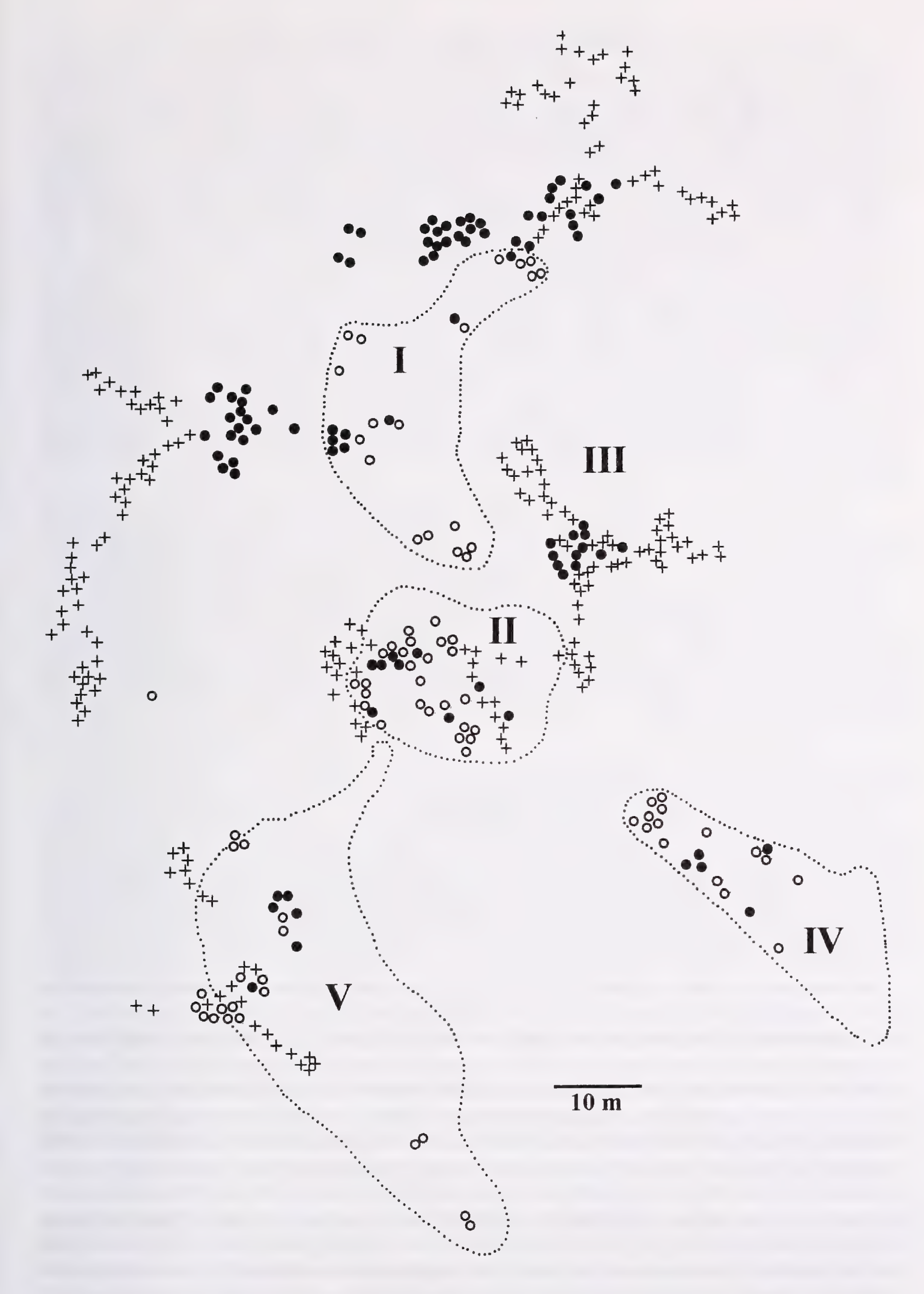


Fig. 2. Dynamics of five mandarine vole burrows (June–July, late September 1986) as revealed by soil mounds. Dashed lines indicate areas covered by old mounds in early June. Open circles, solid circles, and crosses indicate new mounds plotted in June, July, and September, respectively.

Group territory sizes and dynamics

At the very beginning of the spring trapping session (mid-April 1991) most part of the area under study was covered with mounds of soil indicating that many burrows were inhabited in March. For 20 well-distinguishable burrows the mean size (± SE) determined by the old mounds was 265 ± 55.9 m^2. However, the following observation revealed only 4 burrows where the fresh mounds had appeared; their areas determined by the mounds registered from 20 April up to 20 May were 110 m^2 (inhabited by a single female with young), 70, 15, and 25 m^2 (each inhabited by a pair of adults). The fifth burrow was founded by a single male in early May and reached 25 m^2 by 20 May.

During the summer sessions of 1986 and 1992, a total of 14 burrows were followed through at least one month, most of them from the first decade of June up to the first decade in July. For this period, the mean size (± SE) of the burrows consisted of 142 ± 32.4 m^2 (range 50–370 m^2, n = 13, pooled data of 1986 and 1992). The fourteenth burrow was extremely large; by July it reached about 600 m^2 (this value is not included in the calculation) with the family consisting of 22 individuals. In late July this family had divided into two, which began to exploit the different parts of the enormous territory. By October these burrows were separated from one another by a distance of over 40 m (Fig. 2, burrow I).

In early–mid July the dispersal of young was attended by the emergence of new small burrows (e.g., burrow III, Fig. 2). Three burrows that were monitored from the first mounds grew very rapidly: within two weeks they reached 15, 15, and 54 m^2. By late September the soil mounds in smaller burrows covered areas of 112 and 140 m^2 (1986).

In late summer-late autumn a considerable increase of the burrowing activity was observed. During fall daily 3–6 (up to 12) fresh mounds per burrow were recorded, e.g. equivalent to only 1–3 (up to 6) mounds per burrow in summer. An area exploited by a family group from mid-August up to mid-September 1993 averaged (± SE) 177 ± 32.0 m^2 (n = 11), range 80–330 m^2.

Discussion

From the trapping data results, the basic type of spatial organisation for *L. mandarinus* is group territoriality. The mating system varies from polygyny to monogamy, the former predominating. Mateships are prolonged and appear to dissolute if some of the mates die. Young born in spring as well as later stay with their parents for a long time. As has been shown in the laboratory (Zorenko et al. 1994; Smorkatcheva et al. 1997), the life cycle of *L. mandarinus* is characterized by rather long intervals between weaning (about 19–22 days) and the earliest age of fertility (55–60 days for males, 36–38 days for females). In this study most of the young were known to remain in their natal burrows during this ontogenetic phase. Apparently, they help their mother rear subsequent 1–2 litters both by direct and indirect parental investment as it was observed in the laboratory (Zorenko et al. 1994). For reproduction, sons apparently must leave the natal territory. According to trapping data young males seem to disperse at the age of 45–70 days, i.e. about the time of puberty. Daughters may stay in the natal territory as nonreproductive female, stay and reproduce, or disperse. In contrast to males no young female was recorded as migrant, although two individuals were known to settle at new sites. Several females were captured in their natal burrow as reproductive. *L. mandarinus* display strong incest-avoidance and contact with strange male is necessary for reproductive activation of young females (Smorkatcheva et al. 1997). Evidently females wait for a mate in their natal territory for some time after becoming physiologically fertile. Meanwhile, they increase their inclusive fitness by helping kin individuals and receive a chance to inherit the parental burrow and

territory thereby, avoiding risks involved in dispersal. The change of sire appears to be the necessary condition to realise this chance. Most of polygynous groups are likely formed in such a way.

The question remains open about the proximate causes of natal dispersal in *L. mandarinus*. From our preliminary laboratory data only amicable interactions occur between family members independent of their age. These observations do not support the hypothesis that aggression from adult members of the group forces the young to disperse (Christian 1970; Anderson 1980; Boonstra et al. 1987). It is more probable that different factors trigger the dispersal in the two sexes. Internal physiological cues might be sufficient to promote male dispersal. In female ontogeny not the "dispersal phase", but the "mating or waiting for a mate phase" seems to be present. Natal dispersal of females was shown to be preceded by maturation and mating in *M. arvalis* (Boyce and Boyce 1988). Hormonal events induced by copulation probably account for strong female bonding to male in monogamous *M. ochrogaster* (Carter and Getz 1993). In the latter species, the important role of non-resident, non-paired males in reproductive activation of young females was clearly demonstrated (Carter et al. 1980; McGuire and Getz 1991; McGuire et al. 1990; Lyons and Getz 1993). For *L. mandarinus*, I hypothesise that not only non-resident males activate the reproduction, but also may promote the dispersal of young females if their mate does not remain with their family after copulation.

If this hypothesis is true the following predictions should be realised:

(i) the higher the number of non-paired males in a population, the greater the proportion of young females becoming reproductive

(ii) the higher the mortality in fathers, the greater the proportion of daughters reproducing within the natal territory.

Thus, (iii) if the survival of mated males is high and numerous unmated males are present in a population, then high levels of female natal dispersal and increasing numbers of new breeding units should be expected.

These assumptions should be examined both in field demographic studies and in laboratory ethology experiments.

Thus, in nature *L. mandarinus* exhibits group territoriality, prolonged pair-bonding, and parent-young relationships. Previously the species was reported to display the characters of K-strategy (small litter size, slow development and sexual maturity, incest-taboo), paternal care activity, care by weaned young of pups, long latency, and low level of copulatory stimulation (Zorenko et al. 1994; Smorkatcheva 1997). All of these traits are usually attributed to monogamy (Kleiman 1977; Dewsbury 1990). However, *L. mandarinus* combines a monogamous system of rearing with a polygynous system of grouping and mating. It is this combination of traits that underlies the high level of sociality in the mandarine vole.

The social structure of this species appears to be similar to that of the prairie vole *M. ochrogaster* and the pine vole *M. pinetorum*. The latter two species are the classical examples of monogamous microtines, although both display communal reproduction under certain conditions as well (Gavish et al. 1981; Fitzgerald and Madison 1983; Getz et al. 1990). The tendency of the young to philopatry and cooperative breeding has been found in the prairie vole (McGuire et al. 1993) as well as in the pine vole (Fitzgerald and Madison 1983). These examples of monogamous or communal breeding units in voles are often considered to be exceptional (e. g. Anderson 1980; Wolff 1985; Nelson 1987). However, the analysis of the available data dealing with the spatio-social structure for Old World microtines shows that this pattern is not at all that rare. Apparently, it is typical for *Microtus socialis* (Shchipanov and Kasatkin 1996), *Eolagurus luteu*s (Labunetz 1968; Shubin 1974), *Prometheomys schaposchnikovi* (Gambaryan et al. 1957; Turov 1926), *Lasiopodomys brandti* (Khrustzelevski 1954 a; Grosse et al. 1984; Dmitriev et al. 1992; Xin-Rong et al. 1998), and *Ellobius talpinus* (Shubin 1961; Zubko and Ostryakov 1961).

The mating system of *M. ochrogaster* is generally believed to be an adaptation to homogeneous, stable, low-food habitats where the females are widely dispersed and it is better for a male to guard a selected mate instead of searching for others (GETZ 1978; NELSON 1987; GETZ and CARTER 1996). However, the benefits associated with living in groups are unclear for this species (GETZ et al. 1990; MCGUIRE and GETZ 1995). In *M. pinetorum* and *L. mandarinus* it is the fossorial habits that might explain prolonged pair-bonding as well as phylopatry and sociality if we presume that:

(i) the risk of above-ground wandering is especially high for the fossorial animals;

(ii) the construction of new tunnels is also associated with high costs (POWELL and FRIED 1992);

(iii) the male and the philopatric offspring gain indirect fitness benefits by forage tunnel building and maintenance and probably care for pups (POWELL and FRIED 1992).

However, the statement of ELWOOD (1983) that direct care of offspring (huddling, grooming, retrieving) by a male is rather a result of his staying with the mother appears to be likely for voles.

Thus, the set of traits mentioned above (prolonged strong pair-bonding, retention by mature offspring, care of the offspring by all group members) is not specific only for fossorial microtines but is expected to be typical for all of them. It seems to be true for a few species other than *M. pinetorum* and *L. mandarinus*, whose social pattern has been reported, *Prometheomys schaposchnikovi* (TUROV 1926) and *Ellobius talpinus* (SHUBIN 1961; ZUBKO and OSTRYAKOV 1961).

When the group composition of *L. mandarinus* is compared with that of other social microtines, the former appears to resemble most closely *L. brandti* by the complexity and large size of units. In both species the summer groups consist of 6–8 individuals (up to 20–25) and often include several reproductive females and 2–3 generations of youngs; the division of oversize families into several distinct ones has been discribed previously (GROSSE et al. 1984; DMITRIEV et al. 1992; XIN-RONG et al. 1998; this study). In contrast to this, the social groups generally contain 2–3 reproductive animals with only a few offspring in *Microtus socialis* (SHCHIPANOV and KASATKIN 1996), *M. ochrogaster* (GETZ et al. 1993), *M. pinetorum* (FITZGERALD and MADISON 1980), and *Eolagurus luteus* (SHUBIN 1974). The analysis of data available on sexual maturity in voles reveals a second trait that *L. mandarinus* and *L. brandti* have in common. This is the great obligatory delay of fertility with respect to weaning. In *Lasiopodomys* the minimal age of fertility in females has been reported as 35–40 days (*L. mandarinus* see ZORENKO et al. 1994; *L. brandti* see ZORENKO and JAKOBSONE 1986), males maturing even later. This phase of ontogeny may be considered as “period of helping”. In most studied microtines from grasslands, both the delay of maturation and dispersal are facultative with the earliest conceptions in females occurring at about weaning or soon after, at 15–30 days (POKROVSKI 1967; SHUBIN 1974; NADEAU 1985; BOYCE and BOYCE 1988). The exceptions are *M. pinetorum* (SCHADLER and BUTTERSTEIN 1979) and probably, *Ellobius talpinus* (ZUBKO and OSTRYAKOV 1961).

Finally, the third trait of *Lasiopodomys* apparently associated with a high level of sociality, is the predominance of tactile contacts during interactions of these voles.

Thus, the genus *Lasiopodomys* seems to be among the most social of voles. The genus now occurs in the open, highly seasonal grasslands of Central Asia. The colonial organisation of *L. brandti* is thought to be associated with (1) construction of complex by extended winter burrows, (2) storage of winter-food supplies in snow-free steppe, and (3) use of acoustic communication like ground squirrels to avoid predators (NAUMOV 1955; NIKOLSKI 1979; GROSSE et al. 1984). The mandarine vole has solved both the problem of predators and that of winter storage by the transition to subterranean existence and foraging. Moreover. the northern subspecies *L. mandarinus vinogradovi* presents an exceptional example of the tendency towards monophagy, that is rare among voles (the only known monophagous species is *M. breweri*, ROTHSTEIN and TAMARIN 1977) as well as

among the fossorial mammals (Orlov 1978; Nevo 1995). At the same time, neither its appearance nor its skull and bones of the extremities seem to demonstrate significant morphological adaptations to a fossorial mode of life. It can be hypothesized that the high level of sociality was characteristic of the ancestral above the ground form and represented the precondition to occupy the recent niche. Probably it is the collective tunnel construction that allows the mandarine voles to feed on the dispersed large roots, as is accepted for mole-rats Bathyergidae (Jarvis 1981; Lovegrove and Wissel 1988).

Acknowledgements

I thank Ekatherine Tsytsulina for her assistance in the field and am also grateful to Dr. Natalia Ambramson for reviewing the English version of the manuscript.

Zusammenfassung

Soziale Organisation der Mandarin-Wühlmaus (Lasiopodomys mandarinus) während der Reproduktionsperiode

Das Sozialsystem in freilebenden Populationen von *Lasiopodomys mandarinus* wurde im Selenginski Distrikt in Burjatien mit Markierungs-Wiederfang-Methoden untersucht. Mandarin-Wühlmäuse lebten in umfangreichen Familiengruppen. Die Mitglieder einer Gruppe waren streng an einen gemeinsamen Bau gebunden. Die Gruppen bestanden im Sommer aus einem reproduzierenden Männchen, 1–5 reproduzierenden Weibchen und von 1–3 Generationen von Jungtieren; durchschnittlich fanden sich 8,7 Individuen pro Bau (Umfang 3 bis 22). Die meisten Nachkommen blieben im Elternterritorium wenigstens 50 Tage lang. Keines von 72 jungen Männchen und nur drei von 73 jungen Weibchen begannen sich im Geburtsbau zu vermehren. Der Wechsel des Vatertieres ist wahrscheinlich eine wichtige Bedingung für die reproduktive Aktivierung von philopatrischen Töchtern.

Folglich zeigt *L. mandarinus* einen hohen Grad an Sozialität, der auf gemeinsamer Jungenpflege und verlängerten Paarbindungen sowie auf verlängerten Bindungen zwischen Eltern und Jungtieren begründet ist. Diese Merkmale werden in der Literatur auch für die Art *Lasiopodomys brandti* beschrieben. Vermutlich war diese soziale Organisation für die nicht subterrane Anzestralform der beiden Arten typisch und die Voraussetzungen dafür, die Nische eines unterirdischen *Stenophagen* zu besetzen.

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Z. Säugetierkunde **64** (1999) 356–362

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Allozyme variation of Cottontail rabbits (*Sylvilagus*) from Mexico

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Receipt of Ms. 27. 11. 1998
Acceptance of Ms. 08. 06. 1999

Abstract

We examined the allozyme variation of cottontail rabbits of the genus *Sylvilagus* from Mexico, and described their genic relationships. Samples of kidney and heart were run in horizontal starch-gel electrophoresis to assess the variation of 23 presumptive loci, and the BIOSYS-1 software was used to compute estimates of genic variation. Results showed that 60.8 % of the loci were polymorphic. *S. floridanus* was the most genically variable rabbit as revealed by mean number of alleles per locus and percentage of polymorphic loci. The fixation index showed genetic differentiation among species. The smallest genetic distance was between *S. floridanus* and *S. brasiliensis* whereas the largest one was between *S. mansuetus* and *S. audubonii*. A phenogram showed *S. mansuetus* branching out first, *S. audubonii* next, and finally *S. floridanus* and *S. brasiliensis* together. In conclusion, *S. floridanus* showed the largest genic variation, *S. mansuetus* was the most distinctive rabbit, and *S. audubonii* and *S. brasiliensis* were the most closely related species.

Key words: *Sylvilagus*, cottontail rabbits, allozymes, electrophoresis, Mexico

Introduction

Cottontail rabbits of the genus *Sylvilagus* are a speciose group that occurs in the New World (Hoffmann 1993). Unfortunately, genetic variation and species relationships within the genus have been barely examined (Scribner and Warren 1986). Reports in the literature on these topics are limited to scarce and scattered references. This is remarkable if we consider the high species richness and population abundance of this genus in North America (Chapman and Ceballos 1990).) Just the Mexican territory, for instance, hosts eight species of *Silvilagus*, four being endemics (Cervantes et al. 1994). The genetic variation of Mexican cottontail rabbits still remains unexplored.

Genetic distance estimates are available for few lagomorph species (Glover et al. 1977; Grillitsch et al. 1992). Only recently, Halanych and Robinson (1997) provided useful information to gain insight into the evolutionary history of some cottontail rabbit species using sequence data from mtDNA.

Sylvilagus floridanus, a cottontail species occurring in Mexico, is genetically variable in Maryland, U.S.A., due to its intensive introduction to that state (Chapman and Morgan 1973; Morgan and Chapman 1981). Isolated populations of the same species in Texas, U. S. A., are genetically differentiated and characterized by periodical high dispersion rates and low genetic flow due to agricultural land use (Van Den Bussche et al. 1987). *S. audubonii* from Texas, another cottontail rabbit occurring in Mexico, displays a

0044-3468/99/64/06–356 $ 12.00/0

high genetic similarity to Texan populations of *S. floridanus*, although no gene flow between them is expected to take place (Scribner and Warren 1986).

These data thus suggest the presence of genic variation within and among species of *Sylvilagus* and may provide an estimation of relationship between species. Therefore, the purpose of this study is to examine the allozyme variation of selected species of Mexican *Sylvilagus*.

Material and methods

Rabbits were collected with a shotgun. Specimens of black-tailed jackrabbit (*Lepus californicus*) from a Mexican locality were included as outgroup. Samples of heart, kidney, and liver were removed and immediately frozen in liquid nitrogen. All specimens were preserved as standard museum vouchers and deposited in the mammalian collection (Coleccion Nacional de Mamiferos, CNMA, formerly IBUNAM) of Instituto de Biologia, Universidad Nacional Autonoma de Mexico, in Mexico City, Mexico.

Localities are listed by species and sample sizes are indicated in parenthesis as follows. *Sylvilagus floridanus*: 14 km W Villa de Arista, Municipio Moctezuma, San Luis Potosi, Mexico, 1620 m (2); 2 km W Santa Maria del Mar, Municipio Juchitan, Oaxaca, 5 m (3); 10 km NW + 2 km E La Rosa Amarilla, Municipio La Manzanilla, Jalisco, Mexico, 2050 m (3); 11 km E + 1.5 km N San Jose de Gracia, Municipio Marcos Castellanos; Michoacan, Mexico, 2100 m (3). *S. audubonii*: 140 km NE Gomez Palacio, Municipio Mapimi, Durango, Mexico, 1189 m (3). *S. mansuetus*: Isla San Jose, Municipio La Paz, Baja California Sur, Mexico, 5 m (3). *S. brasiliensis*: El Chajul, Municipio Ocosingo, Chiapas, Mexico (1); km 35 road Catemaco-Balzapote, Municipio Catemaco, Veracruz (1). *L. californicus*: same locality as that for *S. audubonii* (2).

Homogenates of kidney and heart were analyzed for electrophoretically detectable protein variation and prepared according to the methods of Selander et al. (1971). Procedures for horizontal starch gel electrophoresis also followed those of Selander et al. (1971).

A total of 23 presumptive loci were examined as follows (abbreviations and IEC numbers follow Harris and Hopkinson 1976): buffer system tris-citrate I (pH 6.7–6.3) was used for malate dehydrogenase (MDH-1, MDH-2, 1.1.1.37), lactate dehydrogenase (LDH-1, LDH-2, LDH-3, 1.1.1.27), acid phosphatase (ACP, 3.1.3.2), glucose-phosphate isomerase (GPI, 5.3.1.9), 6-phosphosphogluconate dehydrogenase (PGD, 1.1.1.44), glucose dehydrogenase (GDH-1, GDH-2, 1.1.1.47), purine nucleoside phosphorylase (NP, 2.4.2.1), and general proteins (GP); buffer system tris-citrate II (pH 8) for malic enzyme (ME-1, ME-2, 1.1.1.40), L-glutamate dehydrogenase (GLUD, 1.4.1.3); buffer system PGI-potassium phosphate (ph 6.7) for isocitrate dehydrogenase (ICD, 1.1.1.42), aldolase (ALD, 4.1.2.13), superoxide dismutase (SOD, 1.15.1.1), xantine dehydrogenase (XDH, 1.2.3.2); buffer system tris-malate EDTA (pH 7.4) for sorbitol dehydrogenase (SDH, 1.1.1.14), hexokinase (HK, 2.7.1.1); and buffer system litium hydroxide (A = 10 %, B = 90 %) for alcohol dehydrogenase (ADH, 1.1.1.1), and esterase (EST, 3.1.1.1).

Alleles at each locus were designated by mobility relative to the most common allele at that locus. Results were summarized in the form of individual genotypes by locus for each individual.

Estimates of allelic frequencies, polymorphism, heterozygosity, Wright's (1965) F-statistics, coeffcients of genetic distance (D) of Rogers (1972) and of unbiased distance (D) of Nei (1978) were computed using the BIOSYS-1 program of Swofford and Selander (1981). The coeffcients of genetic distance were calculated with the inclusion of monomorphic loci. Clustering of distance matrices was performed using the unweighted pair-group method with arithmetic averages procedure (UPGMA; Sneath and Sokal 1973; Swofford and Selander 1981).

Results and discussion

Of the 23 loci examined electrophoretically, 14 (60.8 %) were polymorphic (Tab. 1), whereas GP, ME, GDH-1, ADH, MDH-1, LDH-2, GPI, SOD, and ACP were monomorphic. Rare variants (frequency of the most common allele as greater than 0.95) were

Table 1. Alleles (a–d), allele frequencies (in parenthesis), sample size (n), average number of alleles per locus (AVER), percent of polymorphic loci (POLY), and expected average individual heterozygosity (HETE) for leporids (*Sylvilagus mansuetus*, *S. floridanus*, *S. audubonii*, *S. brasiliensis* and *Lepus californicus*) from Mexico. Only polymorphic loci (14 out of 23) are listed. Estimate of POLY includes only those loci for which dominant allele has a frequency less than 0.95. See text for loci abbreviations.

Locus	*Sylvilagus mansuetus*	*Sylvilagus audubonii*	*Sylvilagus brasiliensis*	*Sylvilagus floridanus*	*Lepus californicus*
GLUD	b	b	b	a (0.091) b (0.633) c (0.273)	b
ICD	c	c	c	a (0.091) b (0.182) c (0.720)	c
6PGD	a (0.667) b (0.333)	a	a	a	a
GDH-2	b	b	b	b	a
MDH-2	a (0.333) b (0.667)	b	b	b	b
NP	b	b	b	b	a
ME-2	b	b	b	b	a
LDH-1	b	b	b	a (0.125) b (0.875)	b
LDH-3	b	b	b	b	a
ALD	c	b (0.677) c (0.333)	c	b (0.125) c (0.875)	a a
XDH	b	b	b	b	a
HK	a	a	a	a	b
SDH	a	a	a	a	b
EST	b	a	a	a (0.667) c (0.333)	d
n	3	3	3	8	2
AVER	1.1	1.0	1.0	1.3	1.0
POLY	8.7	4.3	0.0	21.7	00
HETE	0.046	0.023	0.000	0.084	0.000

not present. The locus with the highest number of alleles per locus (= 4) was EST, followed by ALD, ICD, and GLUD (= 3). All loci appeared as single banded homozygotes.

Among the polymorphic loci, seven were polytypic among species of *Sylvilagus* whereas the other seven (GDH-2, ME-2, NP, LDH-3, XDH, HK, and SDH) were fixed for the same allele in all species of *Sylvilagus* (Tab. 1). All loci were monomorphic in *S. brasiliensis* and *L. californicus.*

Sylvilagus floridanus showed a slightly larger average number of alleles per locus (Tab. 1). Proportions of polymorphic loci (95 % criterion) averaged 8.7 among *Sylvilagus* species and ranged from 0 to 21.7. *S. floridanus* also displayed the highest polymorphism value and alternate alleles at four loci (GLUD, ICD, LDH-1, EST). Therefore, *Sylvilagus floridanus* was the most genically variable rabbit.

This is similar to what has been found in several localities of the United States of America for the same species (MORGAN and CHAPMAN 1981; SCRIBNER and WARREN 1986; VAN DEN BUSSCHE et al. 1987). For instance, populations of *S. floridanus* and *S. audubonii* from Texas displayed 33 and 25 % of polymorphism, respectively (SCRIBNER and WARREN 1986). On the other hand, polymorphism recorded in brown hares (*Lepus europaeus*)

from Central Europe was 16.3 % (HARTL et al. 1990). In contrast, no polymorphic loci for *S. brasiliensis* was recorded herein.

In our study no rabbit species showed heterozygote individuals. Similarly, heterozygote deficiencies were noted for populations of *S. floridanus* from Texas (VAN DEN BUSSCHE et al. 1987), although previous studies of *S. floridanus* and *S. audubonii* revealed fair amounts of heterozygosity (MORGAN and CHAPMAN 1981; SCRIBNER and WARREN 1986). Selected populations of the European wild rabbit (*Oryctolagus cuniculus*) from East Anglia, England, also showed heterozygote deficiencies at most loci (SURRIDGE et al. 1998). Moreover, low levels of heterozygosity were reported in pikas (*Ochtotona princeps*) from Colorado, U.S.A. (GLOVER et al. 1977).

The expected genic heterozygosity for *S. floridanus* calculated from Hardy-Weinberg assumptions was 8.4 % (Tab. 1), whereas the mean value for vertebrate populations is 5–6 % (SELANDER and JOHNSON 1973). In contrast, expected figures for *S. mansuetus* and *S. audubonii* were lower (4.6 and 2.3 %, respectively).

Sylvilagus species occurring in Mexican territory thus show detectable protein variation. The extent of variation is, however, comparatively low.

Our estimates of genetic distance (NEI's, 1978, unbiased distance) between species turned out to be relatively low compared to those of other vertebrate populations. Our results are comparable to those found for conspecific populations whose coefficients of similarity are generally at the 0.90's level (SELANDER and JOHNSON 1973; HARTL et al. 1990). This is particularly true for genetic distances among the species pairs *S. audubonii – S. brasiliensis*, *S. brasiliensis – S. floridanus*, and *S. audubonii – S. floridanus* (Tab. 2). Populations of *S. audubonii* from Texas also displayed high genetic similarity (ROGER's similarity index = 0.884) to sympatric *S. floridanus* (SCRIBNER and WARREN 1986). *S. floridanus* from the same region displayed NEI's genetic distances between populations ranging from 0.20 to 0.388 (VAN DEN BUSSCHE et al. 1987).

The lowest genetic distance recorded was between *Sylvilagus floridanus* and *S. brasiliensis* (Tab. 2), the only two cottontail rabbit species that occur as far south as the temperate and tropical habitats of South America. They mostly are allopatric species although they also may be parapatric, seldomly sympatric. In contrast, the largest genetic distance recorded herein was between *S. mansuetus* and *S. audubonii* (Tab. 2), species adapted to xeric conditions and whose ranges are very close.

Sylvilagus mansuetus, once thought to be a subspecies of *S. bachmani*, turned out to be the most distinctive rabbit of the species sample examined (Fig. 1). This cottontail is restricted to a small island of 194 km^2 in the Gulf of California, Mexico. Unfortunately, other than the original description of the species, there are no reports on the relationships of this rabbit to other cottontail rabbits. The mean genetic distance (NEI's, 1978 unbiased distance) between *S. mansuetus* and other *Sylvilagus* species was 0.057. This species dis-

Table 2. NEI's (1978) unbiased distances (above diagonal) and ROGERS' (1972) genetic distances (below diagonal) among leporids (*Sylvilagus mansuetus*, *S. floridanus*, *S. audubonii*, *S. brasiliensis*, and *Lepus californicus* from Mexico.

	Sylvilagus mansuetus	*Sylvilagus audubonii*	*Sylvilagus brasiliensis*	*Sylvilagus floridanus*	*Lepus californicus*
Sylvilagus mansuetus	–	0.071	0.051	0.050	0.599
Sylvilagus audubonii	0.101	–	0.018	0.022	0.559
Sylvilagus brasiliensis	0.072	0.029	–	0.010	0.571
Sylvilagus floridanus	0.103	0.068	0.050	–	0.567
Lepus californicus	0.464	0.430	0.435	0.446	–

played alternate alleles at two loci (6PGD, MDH-2) relative to *S. audubonii*, its nearest geographic sample examined in this study. In addition, these pair of species were fixed for one alternate allele at the EST locus (Tab. 1).

The values of genetic differentiation (Fst) among species were relatively high (Tab. 3), except for four loci (GLUD, ICD-1, 6PGD, and MDH-2). The mean Fst was high too considering all species examined (0.851). When the outgroup (*L. californicus*) is removed from the calculations, the average is lower (about half = 0.462; Tab. 3), but still indicative of substancial species differentiation. This fits that *S. mansuetus*, *S. audubonii*, *S. floridanus*, and *S. brasiliensis* are also morphologically distinctive (CHAPMAN and CEBALLOS 1990). Similarly, populations of *S. floridanus* from Texas revealed a significant degree of genetic differentiation too (VAN DEN BUSSCHE et al. 1987).

Table 3. Fixation index (WRIGHT's Fst) for polymorphic loci calculated among leporids (*Sylvilagus mansuetus*, *S. floridanus*, *S. audubonii*, *S. brasiliensis*, and *Lepus californicus*) from Mexico, and among the same samples excluding *L. californicus*.

Locus	All samples	All samples exclusive of *L. californicus*
GLUD	0.251	0.239
ICD-1	0.177	0.168
6PGD	0.286	0.273
GDH-2	1.000	–
MDH-2	0.286	0.273
NP	1.000	–
ME-2	1.000	–
LDH-1	0.875	0.097
LDH-3	1.000	–
ALD	0.746	0.478
XDH	1.000	–
HK	1.000	–
SDH	1.000	–
EST	0.859	0.771
Mean	0.851	0.462

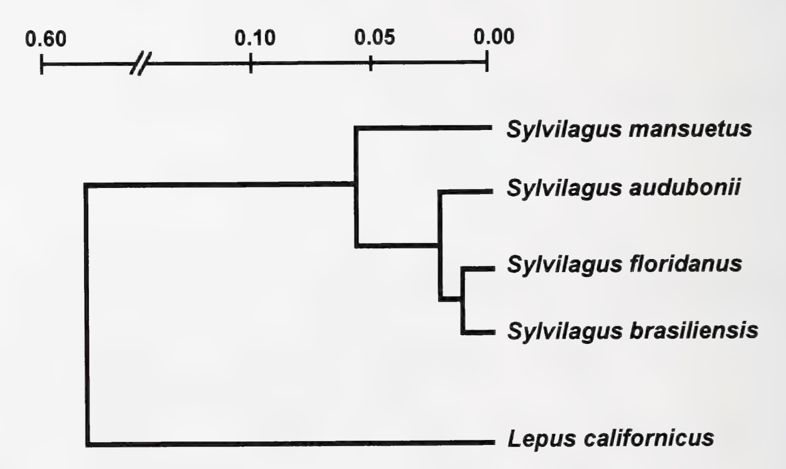


Fig 1. UPGMA tree of leporids (*Sylvilagus mansuetus*, *S. audubonii*, *S. brasiliensis*, *S. floridanus*, and *Lepus californicus*) from Mexico based on NEI's (1978) unbiased distances. The cophenetic correlation coefficient = 0.999.

The UPGMA procedure of a matrix of unbiased distances (Nei 1978) revealed three allozymic groups present within the *Sylvilagus* group (Fig. 1). The first consisted of *S. mansuetus* branching out first (fixed for one allele at the EST locus), *S. audbonii* next, and *S. floridanus* and *S. brasiliensis* together, who were relatively closely allied, and separated by a genetic distance of 0.010. None of these samples was fixed for different electromorphs relative to all of the other *Sylvilagus* samples. This arrangement may not reflect phylogenetic relationships, but allows to understand the overall genetic resemblance contained in the distance matrix computed.

Assessement of the genic relationship of *S. audubonii* to *S. floridanus* herein fit findings on the systematic relationships among ten species of *Sylvilagus* based on diploid chromosomal numbers (Chapman and Ceballos 1990). That is, *S. audubonii* and *S. floridanus* also occur on separate branches of a dendrogram. Similarly, 12S rDNA data showed that *S. floridanus* and *S. audubonii* were not each other's closest relatives in the species set examined (Halanych and Robinson 1997).

Results presented here are the first data set that outline genic relationships among selected species of *Sylvilagus* occurring in Mexico. It is shown that samples of *Sylvilagus* species occurring in Mexico display detectable protein variation, although lower than that reported for other leporid and vertebrate species. On the other hand, *S. mansuetus* is the most genetically distinctive cottontail rabbit examined, whereas *S. floridanus* and *S. brasiliensis* are the most closely related species pair. Although the four species examined are morphologically well differentiated the genetic distances among them are smaller than expected.

Acknowledgements

We thank C. Lorenzo, J. Vargas, F. X. Gonzalez, A. Gonzalez-R., L. Hernandez, A. L. Colmenares, R. M. Gonzalez, J. Martinez, A. Rojas, S. T. Alvarez, and P. Cortes, for assistance in the field and laboratory. This project was supported in part by Universidad Nacional Autonoma de Mexico (grant IN-203793) and by a grant from the Sir Peter Scott Fund, through the Lagomorph Specialist Group of the Species Survival Commission, World Conservation Union. C. Lorenzo provided useful suggestions to earlier drafts.

Zusammenfassung

Allozym-Variation von Wollschwanz-Kaninchen (Sylvilagus) aus Mexiko.

Wir untersuchten die Allozym-Variation von ausgewählten Arten des Wollschwanz-Kaninchens der Gattung *Sylvilagus* aus Mexiko und beschrieben deren genetische Verwandtschaften. Proben von Niere und Herz wurden horizontaler Stärkegelelektrophorese unterzogen, um die Protein-Variation von 23 vermuteten Loci zu bestimmen, und die Software BIOSYS-1 wurde benutzt, um Schätzungen der genetischen Variation zu berechnen. Die Ergebnisse zeigten, daß 60,8 % der Loci polymorph waren. *S. floridanus* war das genetisch variabelste Kaninchen, wie die mittlere Anzahl von Allelen pro Locus und der Prozentsatz von polymorphen Loci zeigten. Der „Fixations-Index" zeigte genetische Differenzierung unter den Arten. Die geringste genetische Distanz bestand zwischen *S. floridanus* und *S. brasiliensis*, die größte zwischen *S. mansuetus* und *S. audubonii*. Ein Phaenogram zeigte, daß *S. mansuetus* als erste Art abzweigt, *S. audubonii* als nächste und *S. floridanus* und *S. brasiliensis* gemeinsam. Schlußfolgernd zeigte *S. floridanus* die größte genetische Variation, *S. mansuetus* war das unterschiedlichste Kaninchen und *S. floridanus* und *S. brasiliensis* waren die am engsten verwandten Arten.

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Z. Säugetierkunde **64** (1999) 363–370

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Allosuckling behaviour in Ammotragus

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Receipt of Ms. 21. 12. 1998
Acceptance of Ms. 20. 08. 1999

Abstract

Allosuckling behaviour is investigated in a captive population of Saharan arrui (*Ammotragus lervia sahariensis*). Allosuckling attempts are sporadic and usually unsuccessful (75%). The age of alien calves is strongly related to the age of allomother calves, and small differences in age between them are associated with successful allosuckling attempts. Young calves are also more successful when attempting allosuckling, although they undergo the most aggressive responses by the allomother. On the other hand, the two adoption instances observed took place in newborn calves. Neither the sex of the calf nor his/her coefficient of relationship with the allomother has any influence on the success of allosuckling. A series of hypotheses is discussed in the light of the results obtained; such as mistaken identification of the mother, kinship and crowded captive conditions.

Key words: *Ammotragus*, ungulates, allosuckling, adoption, maternal investment

Introduction

Adoption has been reported in *Ovis* and *Capra* genera (Hersher et al. 1963; Gubernick 1980) characterized by strong mother-infant bonds (e.g. Schaller 1977; Gubernick, 1981; Romeyer et al. 1993). Non-offspring nursing has been observed occasionally in both domestic and wild sheep (Hass 1990; see also Rowell 1991); allosuckling behaviour reported in the bighorn, *Ovis canadensis* (Hass 1990) and roe deer, *Dama dama* (Birgersson et al. 1991); and both casual allosuckling and adoption are commonly considered to occur in the bison, *Bison bison* (McHugh 1958; Altmann 1963; Lott 1972), and water buffalo, *Bubalus bubalis* (Tulloch 1979; Murphey et al. 1991).

Whenever alloparental care refers to allosuckling, occasional or frequent, costs for the donor (allomother) rise considerably (see Clutton-Brock et al. 1989). Recently, Packer et al. (1992) showed that non-offspring nursing is increased by captivity and in mammalian species that have large litters. These authors also pointed out that in monotocous taxa (those typically giving birth to only one infant) allosuckling is generally rare and females tend to be less tolerant (Packer et al. 1992).

The present study analyses both allosuckling and adoption in an African ungulate, the Saharan arrui (*Ammotragus lervia sahariensis*), a monotocous species with only one twin birth every 4.4 singles (Cassinello and Alados 1996). The aim of this study is to clarify the incidence of allosuckling behaviour in an ungulate social group, attempting to determine whether it is related to mistaken identifications of the mother by the calf, or promoted by either kinship or crowded conditions.

0044-3468/99/64/06–363 $ 12.00/0

Material and methods

Data were collected in a captive population of Saharan arrui which is successfully breeding in captivity at the Estación Experimental de Zonas Aridas (EEZA), Almería, south of Spain (Cassinello and Alados 1996). This population originates from just one male and one female captured in 1975 in the western Sahara. It is suspected that the subspecies is already extinct in the wild (Alados and Vericad 1993). Sampling was carried out from 1990 to 1992 in a herd made up of 17 males and 26 females at the beginning of the study, and 33 males and 43 females at the culmination of the study. The total surface available to the animals was 950 m^2. Detailed information on sampling method and routine can be found in Cassinello (1996), although a general description has been added here.

The animals were identified by means of coloured plastic ear tags, the differing position and shape of these tags determined a number for each individual. Birth date, parturition type (single or twin), sex, identity of father and mother, and inbreeding coefficient were known for each individual. Sampling was carried out during evenings, when females and calves were more active and the great majority of suckling events took place. Focal sampling was used to record mother and calf behaviour (Altmann 1974; Martin and Bateson 1986), each sample being 20 min duration. A sampling period was the total number of focals carried out on a given day. Every female which gave birth during 1990 and 1991 was sampled four times a week during the calf's first two months of life; during the remainder of the lactation period (for the weaning process, see Cassinello 1997 a) sampling was carried out 1.5 times per week. All mother-calf interactions between them and the other group mates were recorded. Suckling events were sampled ad libitum. A total of 26 mother-calf pairs was sampled; 8 calves shared their nursing with a sibling and 18 were single.

Only allosuckling attempts directed towards lactating females were taken into account. For the sake of clarity, throughout this study a calf attempting a suckling event on a lactating female other than his/her actual mother is named an alien calf, and the lactating female an allomother. In relation to the females' responses to the allosuckling attempts, four behaviours were distinguished: aggression, withdrawal, no response and adoption. No response means the allomother did not react when faced with an alien calf's allosuckling attempt, but this lack of response did not imply a successful attempt, as it might fail due to other factors, such as the lack of alien calf's determination while the allomother is engaged in other activities, i. e. feeding; in addition on one occasion a wire fence prevented the alien calf (no. 192) from allosuckling. Also, successful attempts could be followed by allomother rejection (aggression or withdrawal) once she is aware of the alien calf's presence, which might occur a few seconds later, enough time to score a successful event.

The coefficients of relationship (c. r.) between alien calves and allomothers were calculated following Maciejowski and Zieba (1982). The social ranks were calculated for all the lactating females, and the rank given to a particular individual corresponded with the percentage of individuals with a lower dominance status (Cassinello 1995). When parametric tests were used, non-normal dependent variables were transformed according to, e. g., Zar, (1984). Replication was tackled by means of the analysis of intra and intergroup variance, which showed for all the response variables that the intergroup variance was not greater than the intragroup variance, so that all the data were considered as independent.

Results

Allosuckling, carried out by 10 different calves, occurred sporadically in the population under study: only 20 events were registered during the whole sampling period, two of them leading to adoptions (Tab. 1). Taking into account the first suckling attempt which led to an adoption as an allosuckling one, the percentage of occurrence of allosuckling behaviour was as follows: 3.3% of the whole suckling behaviour (20 out of 611 events registered), 1.4% of the successful suckling events (5 out of 357), and 5.9% of the unsuccessful ones (15 out of 254). Allosuckling took place at very different ages, from 0 to 463 days-old (Tab. 1), although the median is 19 days, and the mean 62 days (0 days refers to newborn individuals).

A strong and positive relationship between the age of alien calves and the age of allomothers' calves can be seen first (simple regression: $n = 20$, $r^2 = 0.51$, $P = 0.0004$; Fig. 1).

Table 1. Some characteristics of the allosuckling behaviour observed in the studied population. Response refers to the allomother's reaction against allosuckling attempts. Key: F = female, M = male, S = successful, U = unsuccessful, Adop = adoption, NR = no response, Agg = aggression, and W = withdrawal

Calf number	Calf sex	Allosuckling	Allomother no.	Response	c. r.
149	F	S	26	Adop	0.5759
153	F	S	46	Adop	0.5666
153	F	U	28	NR	0.5434
155	F	S	31	Agg	0.5206
155	F	U	31	W	0.5206
156	M	U	33	W	0.4900
157	F	U	35	W	0.4900
157	F	S	35	W	0.4900
186	F	U	28	Agg	0.6214
186	F	U	21	NR	0.6062
186	F	U	21	Agg	0.6062
186	F	U	26	W	0.5456
186	F	U	64	W	0.5259
188	M	U	17	Agg	0.5153
188	M	U	26	Agg	0.5911
192	M	U	26	Agg	0.5759
192	M	U	36	NR	0.5153
194	F	U	26	Agg	0.5206
194	F	U	21	NR	0.4900
195	F	S	28	Agg	0.5819

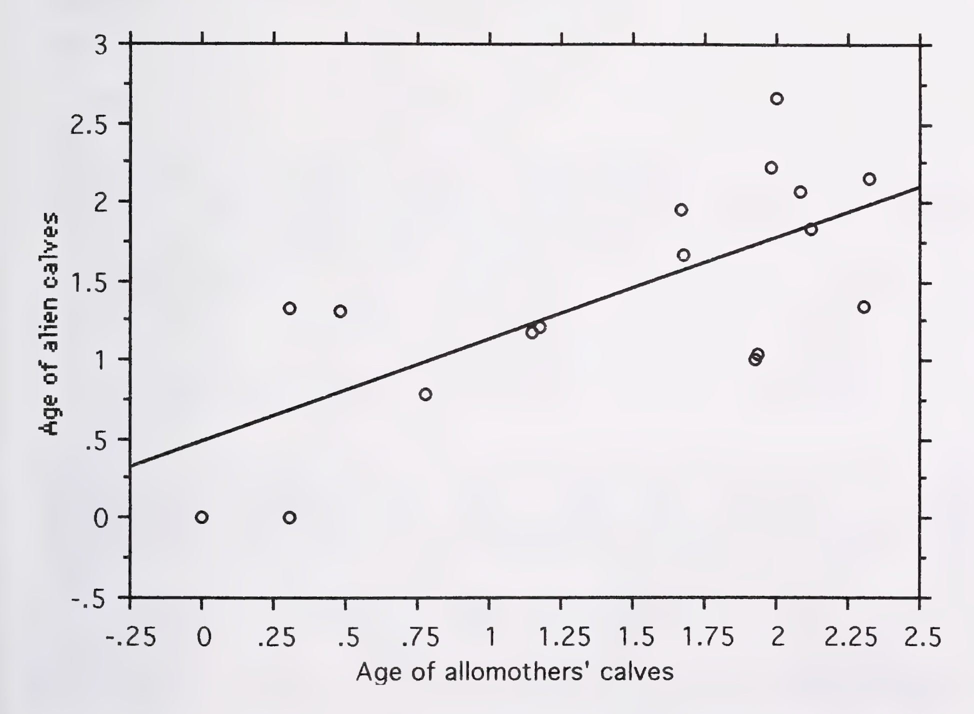


Fig. 1. Relationship between the age of alien calves and the age of allomothers' calves. Age shown is in days transformed into their logarithm to run the simple regression analysis.

However, no relationship was found between the age of alien calves and their coefficient of relationship with the allomothers (n = 18, $r^2 = 0.001$, P = 0.89).

The age of calves who successfully attempted allosuckling (25% of the total attempts) was lower than that of calves who performed unsuccessful allosuckling (successful calves: 8 ± 4 days; unsuccessful calves: 80 ± 30 days; ANOVA: F(1.18) = 10.33, P = 0.005); also, successful allosuckling was observed on mothers who were nursing younger calves (4 ± 2 days) than unsuccessful ones (77 ± 18 days; F(1.18) = 11.00, P = 0.004). Furthermore, the success of allosuckling was greater when the difference in age between alien calves and allomothers' calves was smaller (4 ± 3 vs 66 ± 25 days; F(1.18) = 5.48, P = 0.03). Neither the coefficient of relationship between alien calves and allomothers (F(1.18) = 0.02, P = 0.89) nor the allomothers' social rank (F(1.18) = 1.66, P = 0.21) had any influence on the success of the allosuckling attempts.

Both the mean age of the alien calves and the age of the allomother were significantly different for the four allomother's responses considered; the differences being particularly acute between calves actually adopted (newborn) and the remaining cases (see Tab. 2). The four types of responses showed similar values for the difference in age between alien calves and allomothers' calves (F(3.16) = 0.88, P = 0.47), and the coeficients of relationship between alien calves and allomothers (F(3.16) = 2.93, P = 0.07).

The allomothers' type of response varied depending on their social rank: withdrawals were carried out by low-ranking females (Tab. 3); on the contrary, neither the actual mother's rank nor the rank difference between mother and allomother was related to the latter's response (Tab. 3); although there is a tendency for allomothers of relatively low rank in relation to the actual mother's rank to withdraw when faced with calf's allosuckling attempts (Fisher's post-hoc test: P = 0.06).

A three-fourths majority of the calves who attempted allosuckling was females, but this number was not statistically significant (Fisher's Exact Test: df = 1, P = 0.19). Both males and females attempted allosuckling at the same average age (F(1.18) = 0.11,

Table 2. Mean (± SE) age in days of both alien and allomother's calf in relation to the response of the allomother to the allosuckling attempt. [a]ANOVA: F(3.16) = 7.15, P = 0.003; Fisher's post-hoc test: aggression vs no response P = 0.05, adoption vs the others P < 0.004. [b]ANOVA: F(3.16) = 4.39, P = 0.02; Fisher's post-hoc test: adoption vs aggression P = 0.008, adoption vs no response P = 0.007.

Allomother's response	Alien calf age[a]	Allomother's calf age[b]
Agression	28.5 ± 11	72 ± 24
Withdrawal	58 ± 27	37.5 ± 22
No response	166 ± 102.5	92 ± 43
Adoption	0	0.5 ± 0.5

Table 3. Mean (± SE) mother's rank, allomother's rank, and ranks difference in relation to the response of the allomother to the allosuckling attempt. [a]ANOVA: F(3.16) = 0.91, ns. [b]ANOVA: F(3.16) = 4.20, P = 0.02; Fisher's post-hoc test: aggression vs withdrawal P = 0.007, withdrawal vs no response P = 0.02. [c]ANOVA: F(3.16) = 1.63, ns.

Allomother's response	Mother's rank (A)[a]	Allomother's rank (B)[b]	(A–B)[c]
Agression	58 ± 9	79 ± 4	–21 ± 12
Withdrawal	64 ± 6	53 ± 6	11 ± 7
No response	58 ± 11	80 ± 9	–21 ± 19
Adoption	36 ± 3	56 ± 16	–20 ± 13

P = 0.74). No relationship was found between the sex of the alien calf and the coefficient of relationship with the allomother (F(1.18) = 0.17, P = 0.68). Finally, the success of the allosuckling behaviour (Fisher's Exact Test: df = 1, P = 0.27) and the allomother's responses (Contingency table: df = 3, χ^2 = 1.56, P = 0.67) were not influenced by the sex of the alien calf.

Only once did a permanent adoption event happen in the study population, where a female (no. 26) allosuckled an alien female calf (no. 149) from birth to her premature death. Just after birth, calf no. 153 was unusually adopted during one day by female no. 46; but eventually the allomother stopped nursing the calf which was then nursed by her actual mother (no. 64). Female no. 46 had deserted her twins (calves no. 148 and 149) just after birth, and one of them (no. 148) was killed by female no. 64. Both adoption events happened to female calves whose age was significantly lower than that of the calves which attempted allosuckling (F(1.18) = 14.93, P = 0.001). The coefficients of relationship with the allomothers were slightly higher in the adoption cases (0.57 ± 0.005 vs 0.54 ± 0.01), but the difference was not statistically significant (F(1.18) = 0.84, P = 0.37). Finally, social ranks of adoptive mothers did not differ statistically from those of non-adoptive mothers (F(1.18) = 0.77, P = 0.39).

Discussion

Casual allosuckling has already been reported in *Ammotraus* by Katz (1949) and Haas (1959), and is considered to occur occasionally in ungulates (e. g. Hass 1990). In the study population, a strong relationship is found between the age of alien calves and the age of allomothers; successful allosuckling attempts depending on this relationship. Moreover, young alien calves are more successful when attempting allosuckling; this might be related to an inefficient sort of "labelling" (sensu Gubernick 1980) or the mother's ability to memorize their own calves' signatures (Porter et al. 1991; but see Romeyer et al. 1993); thus, arrui mothers would recognize older calves more easily. Also the older calves' behaviour might account for these results.

Captivity conditions might promote a certain permissive behaviour towards alien infants, as the mothers have unlimited access to food and the costs associated with nursing are diminished (see Packer et al. 1992); also overcrowding conditions may favour this sort of behaviour (Riedman 1982). But, on the other hand, in social herbivores alien calves are usually rejected by females, a behaviour which is expected to be favoured by natural selection (Gubernick 1981; Harper 1981) unless some sort of benefits came along with allomothering, such as those related to kinship selection (Bertram 1976). Furthermore, recent evidence on monotocous mammalian species, where most social herbivores are included, seems to show that they are poorly tolerant of allosuckling behaviour (Packer et al. 1992).

Calves' mistaken identification of their own mothers may be an explanation for allosuckling to occur, although in some instances single alien calves (not used to share suckles) attempted allosuckling when the allomother's own calves were already suckling. Also, allosuckling attempts might be part of calves' learning behaviour, which may be implemented through negative responses.

A rather speculative hypothesis which might explain the origin of this behaviour refers to young arrui calves seeking extra-milk intakes from lactating females other than their mothers, when young calves of similar ages can be mistaken by adult females; thus, the allosuckling behaviour may well be pursued by alien calves to obtain an additional source (Murphey et al. 1991); however, not enough data are available to test this hypothesis.

On the other hand, allomothers' responses against casual allosuckling were particularly aggressive when addressed to young calves; this may indicate that they represent a more serious threat to maternal resources than older calves, perhaps due to their more efficient suckling behaviour (Cassinello 1996). Also, the hypothetical source of error commented above may provoke this strongly agonistic response. Allomothers who displayed the most submissive response (withdrawal) held the lowest social ranks; but the scarcity of data available does not permit any conclusion on this matter.

The lack of any relationship found between the coefficient of relationship and the allosuckling behaviour in the study population of Saharan arrui might be explained by the high inbreeding coefficients that characterize this population (e. g. Cassinello 1997 b), which causes a low variance for this coefficient (c. r. range = 0.13; minimum value = 0.49; maximum value = 0.62). On the other hand, familiarity might also play an important role in the allomother's tolerance towards alien calves (D'Amato 1993), but we have no data yet to support or refute such a hypothesis. It has been found in sheep that even with a high degree of familiarity (i. e. dizygotic twins), mothers can discriminate between lambs; and familiarity tended to reduce the rejection of a twin kept separated from its mother when compared with a totally alien lamb (Romeyer et al. 1993).

The low frequency of occurrence of casual allosuckling behaviour raises the question of costs and benefits to both alien calves and allomothers. It might be postulated that costs to the calf in terms of aggression, chasing, etc. tend to exceed the benefits obtained (milk intake); although no direct measure of such costs/benefits is available.

As for the adoption events observed in the study population, the high degree of relatedness between all of the individuals makes an explanation in terms of kinship selection unsatisfactory. Hass (1990) reported alloparental behaviour in bighorn females which had lost their lambs 3–40 days after parturition, and Rowell (1991) referred to a similar case in sheep. Probably these lactating females were physiologically and behaviourally "primed" for lactation (Oftedal 1985). A painful, distended udder may be the impetus for nursing alien calves, although it cannot explain why these females continue to nurse calves for the entire lactation period (Hass 1990). Moreover, in sheep, as in other mammals (see Gubernick and Klopfer 1981), there appears to be a sensitive period following parturition during which ewes will be responsive to all lambs, since ewes separated from their lambs at birth will still show maternal behaviour towards any lamb within 4–8 h postpartum (Smith et al. 1966; Poindron et al. 1979). In addition, and although Gubernick's (1980) labelling hypothesis has been questioned recently (Romeyer et al. 1993), maternal attachment in ungulates may take some time for the mothers to discriminate between their own and alien calves. In the studied Saharan arrui population, the adoptees were always newborn calves, while the allomothers had just given birth. Allomothers had not lost their calves before adoption took place, so Oftedal's (1985) hypothesis cannot apply here. The adoptees were deserted by their own mothers a few minutes after birth, although in the one-day adoption this abandonment persisted for only one day.

Recently, a new controversy has arisen concerning a hypothetical transmission of phenotypic characters by means of adoption (Avital and Jablonka 1994, 1996; Hansen 1996). In the Saharan arrui, no benefits, in terms of acquiring a higher social status, were observed (Cassinello 1995) during the actual adoption event; moreover, the allomother had to allocate her resources towards the adoptee and her own calf. In sum, the one-day adoption observed might be considered as a temporal allomother's mistake or even tolerance, and the long-lasting adoption might have been provoked by the overcrowding conditions (Riedman 1982) or by the abandoned alien calf which managed to take advantage of a lactating female who had just given birth (Smith et al. 1966).

In conclusion, evidence of allosuckling behaviour in *Ammotragus* is provided, and possible adaptive interpretations postulated.

Acknowledgements

Thanks go to T. Abaigar, M. Gomendio, and two anonymous referees for constructive comments on earlier versions of the manuscript, and to Juan Moreno for translating the abstract into German. During data collection the author enjoyed a predoctoral grant from MEC (PG89 27511603), being currently supported by DGES Project PB96-0880.

Zusammenfassung

Fremdsaugen bei Ammotragus

In einer in Gefangenschaft gehaltenen Population des Mähnenspringers (*Ammotragus lervia sahariensis*) wurde die Milchaufnahme von Kälbern bei fremden Müttern untersucht. Derartige Saugversuche sind selten und gewöhnlicherweise nicht erfolgreich (75%). Das Alter der fremden Kälber ist dem der eigenen Jungtiere ähnlich, doch geringe Altersunterschiede steigern den Erfolg bei Fremsaugaktivitäten. Wenn auch junge Kälber besonders aggressive Reaktionen der fremden Mutter hervorrufen, so sind sie doch bei ihren Versuchen besonders erfolgreich. Es wurden zwei Fälle von Adoption gerade bei neugeborenen Kälbern beobachtet. Weder das Geschlecht, noch der Grad der Verwandtschaft mit der Fremdmutter beeinflussen den Erfolg der Jungtiere bei der Nahrungsaufnahme an fremder Quelle. Im Lichte der erhobenen Befunde werden mehrere Hypothesen diskutiert: Fehl-Identifikation, Verwandtschaft und hohe Populationsdichte in der Gefangenschaft wurden berücksichtigt.

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Z. Säugetierkunde **64** (1999) 371–375
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http://www.urbanfischer.de/journals/saeugetier



ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNGEN

The maned rat, *Lophiomys imhausii* Milne-Edwards, 1867, in Djibouti, NE-Africa (Mammalia: Rodentia: Lophiomyinae)

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Receipt of Ms. 28. 05. 1999
Acceptance of Ms. 23. 08. 1999

Key words: *Lophiomys*, Djibouti, African distribution

The long-haired fur with a contrasting black-and-white facial pattern renders the maned rat, *Lophiomys imhausii* Milne-Edwards, 1867, an unmistakable African rodent (Williams 1967; Haltenorth and Diller 1977; Kingdon 1997). The genus is currently considered to be monotypic, comprising a number of taxa described as species or subspecies (Ellerman 1940; Misonne 1974; Musser and Carleton 1993).

On March 3rd, 1993, two *L. imhausii* were found (by T. K.) in the SW of Djibouti. They lay dead on road some 12 km SW of Ouea on the route from Djibouti to Ali Sabieh. The specimens (an adult and a juvenile or subadult) were not preserved, but both photographed to document the presence of *L. imhausii* in Djibouti (Fig. 1). The habitat where the carcasses were found is a hilly area (ca. 400 m a. s. l.) with open thorn bush (*Acacia mellifera*, *A. tortilis*; Audru et al. 1987) on stony ground. The biology of *L. imhausii* is so little known, that no convincing explanation can be offered for two individuals being accidentally killed close together. They may have been a female followed by an adolescent young.

From distribution records available (see below) the finding of *L. imhausii* in Djibouti extends the species range to the west. However, the appearance of the species in Djibouti surely is not a recent event, but due to more intensively observing Djibouti wild life (Künzel and Künzel 1998).

The distribution range of *L. imhausii* was listed or mapped more or less accurately, totally or in part, by several authors. Its occurrence in Djibouti is not known (Misonne 1974; Simoneau 1974; Musser and Carleton 1993). However, it could possibly be that the brush-tailed porcupine, *Aetherus africanus*, a Central African rain forest dweller included in the Djibouti mammal fauna by Simoneau (1974), in reality was a *L. imhausii*.

The type specimen of *L. imhausii* was bought alive in Aden (Yemen), but with the discovery of the species in Eritrea, the origin of the specimen was assumed to have been somewhere in "Somalia". Until present the existence of the species in the region of the type locality Aden could not be proven. The discovery of skull fragments, dated to the 11th century, in a cave in the Judean Desert near the Dead Sea was related neither to a palaeontological nor an archaeological context (Dor 1966), and thus it cannot be excluded to have been an imported animal. Further indications for the existence of *L. imhausii* in Arabia (Kingdon 1990) cannot be substantiated at present.

We present a detailed map of the species' African range (Fig. 2), preferring either original sources or reliable compilations. The species is actually known from:

0044-3468/99/64/06-371 $ 12.00/0





Fig. 1. *Lophiomys imhausii*, adult (above) and adolescent (bottom), dead on road, SE-Djibouti, 3. March 1993. Photos: Th. Künzel.

Sudan: Peters (1867): Jebel Maman, 16.16. N–36.48. E, N of Kassala. Giglioli (1881): (Jebel) Eskanid, Red Sea Hills between Suakin and Sinkat. Setzer (1956): near Port Sudan. Misonne (1974) erroneously gives SE-Sudan (instead of NE) as the species range in this country. Records available for Eritrea and Ethiopia were mapped by Yalden et al. (1976). Somalia: Giglioli (1881): Somali coast. (Peel 1900: mentions "Sheikh" as a locality for *L. imhausii*, but does not indicate whether this is [Upper] Sheikh in Somalia or Sheikh [Hussein] in Ethiopia). Drake-Brockman (1910): Burao; Upper Sheikh. Simonetta (1963), Roche (1976): Jesomma, 04.03. N–45.44. E, between Bulo Burti and El Bur. Si-

MONETTA et al. (1978): Hargeisa and Berbera. Kenya: ANDERSON and DE WINTON (1902): Ravine Station, Mau Distr. THOMAS (1905): Elburgon, Mau Forest; between Londiani and Lumbwa, Mau Forest. THOMAS (1910): near Njoro, Mau Forest; Nakuru, Rift Valley; Mutaragwa (= Ndaragwa, 00.07. S–36.37. E), 9 000 ft, Aberdare Mts. DOLLMAN (1911): Solai, 00.07. N–36.12. E. HELLER (1912): Mt. Gargues (Uaragess), 6 000 ft, Mathews Range. LÖNNBERG (1912): Mau Escarpment. KOLLMANN (1913): Mt. Kenya, 2 400 m. HOLLISTER (1919): Naivasha Escarpment; W-side Mt. Kenya, 8 500 ft. GOLDFINCH (1923): Aberdare

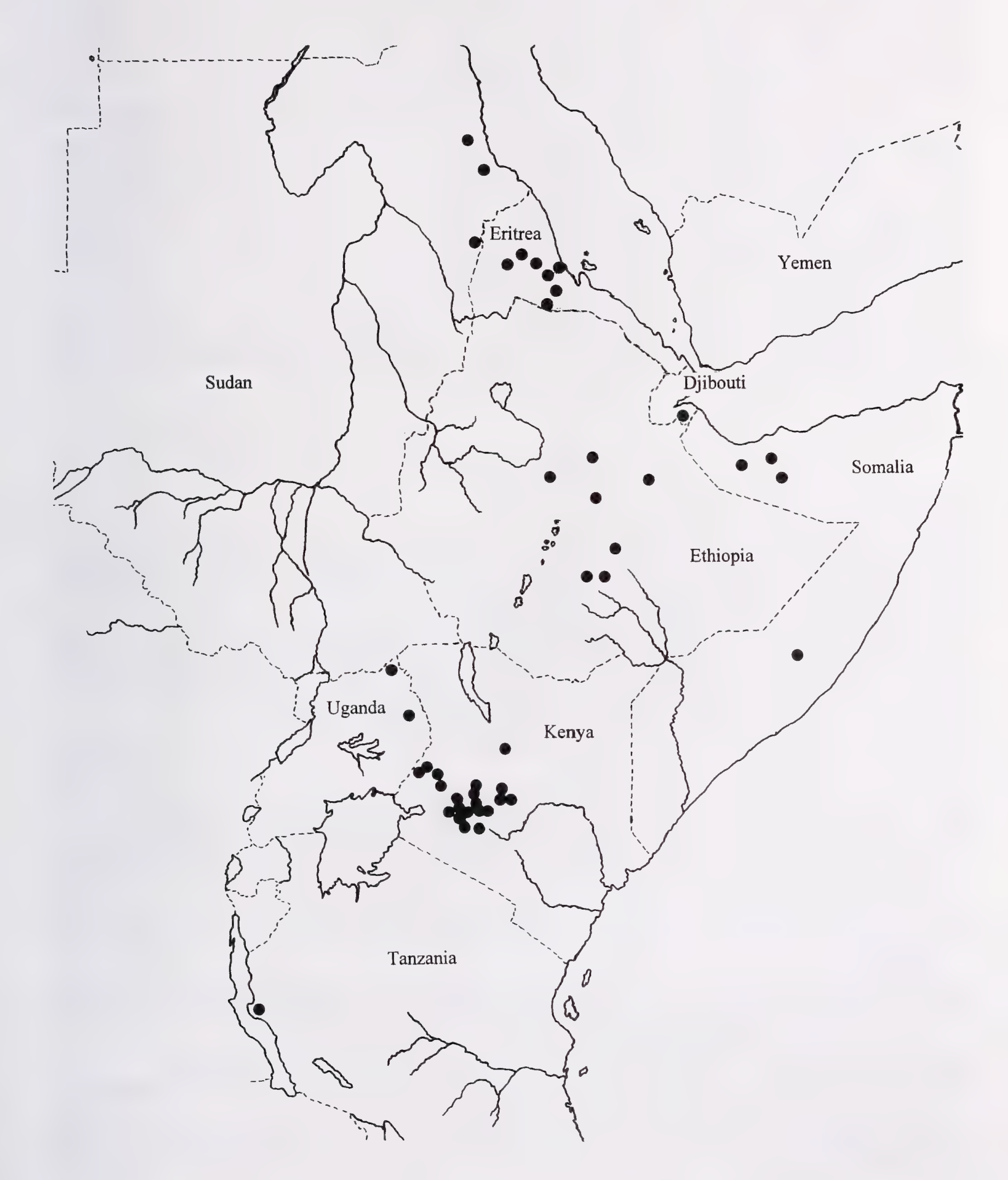


Fig. 2. Distribution of *Lophiomys imhausii*; for details see text. In the Kenyan range some symbols cover one to three neighbouring locality records.

side of Nakuru. Ruxton (1926): Cherengani Hills. Arthur (1957): Nanyuki, W-side Mt. Kenya. Johnson (1960): Sabukia, 00.00.–36.14. E. Williams (1967): Mt. Elgon. Guggisberg (1968): near Rongai, W of Nakuru; near Eldoret, Uasin Gishu Plateau. Delany (1975): Trans Nzoia, 1 900 m. Wahlert (1984): Laikipia Escarpment, 0.28. N–36.07. E; Laikipia Forest; Nyeri; N-Abderdares; SW-Kenya. Johnson et al. (1993): Muruku Sublocation, 0.35. N–36.15. E, Laikipia Distr. Uganda: Thomas (1906) listed *L. imhausii* for Uganda, which at that time comprised W-Kenya east to the Rift Valley, and is based on a specimen from Ravine Station, Mau Distr., collected by the then Governor of Uganda, F. J. Jackson (see Anderson and De Winton 1902). Kingdon (1974): Moroto, Karamoja; in map (: 525) the Kidepo area in the NE is plotted [original source not traced]. Tanzania: Kingdon (1974): 525, map; 1997: 188, map: Mahali Mts., E of L. Tanganyika.

As far as the fossil history of the genus *Lophiomys* is documented (Topacevski and Skorik 1984; Wahlert 1984; Aguilar and Michaux 1990) it is an immigrant from Asia and its range became restricted to northeastern Africa. This could be attributed to geological and climatic factors (erosion and vegetational changes). Modern records available indicate that the recent species range appears to be fragmented, at least between Dibouti-Somalia and Ethiopia by the Danakil Desert, and between Ethiopia and Kenya by an extensive arid region. Furthermore, it seems that in the southern part of the species range denser forests are inhabited (Mahali Mts., Mt. Kenya, Aberdares, Mau) than in the north (Eritrea, Red Sea Hills). However, the collecting data equally indicates that more intensive search for *L. imhausii* may interconnect some of the known disjunct populations.

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Z. Säugetierkunde **64** (1999) 376–379
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Faecal analysis of the edible dormouse (*Glis glis*) in the northwest Iberian Peninsula

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Receipt of Ms. 15. 04. 1999
Acceptance of Ms. 14. 07. 1999

Key words: *Glis glis*, diet, faecal analysis, Galicia, Spain

The edible dormouse (*Glis glis* Linnaeus, 1766) is a tree-dwelling and exclusively crepuscular/nocturnal rodent. To date, there have been few studies of its diet in optimal habitats, and all such studies have been based either on analysis of stomach contents (Kahmann 1965; Holisova 1968; Castroviejo et al. 1974; Gigirey and Rey 1998) or on field observations, which require considerable effort and are very difficult in view of the species' habits (Vietinghoff-Riesch 1960; Rodolfi 1994). The aim of this study is to investigate the diet of *G. glis* through faecal analysis.

The study was carried out in the Parque Natural de Invernadeiro (Galicia, NW Spain). The study area (1000–1200 m) is a 4.1 ha area of mixed broad-leafed woodland, mainly of *Quercus robur*, with a well-developed understorey.

The diet studies were based on the analysis of 293 droppings collected in the study area in 1997, over the period June-October inclusively. All droppings were obtained inside or on top of nest-boxes specifically designed for *G. glis*. The model is similar to that of Morris et al. (1990) for *Muscardinus avellanarius*, but larger in size.

A total of 47 nest-boxes were distributed throughout the study area at regular intervals of about 25 m, at a height of 2–3 m above ground, and they were checked monthly. Since nest-boxes were not occupied until July, in May and June it was necessary to use Sherman traps, baited with apple and peanut butter, to obtain the droping. It should be stressed that this may have had some influence on the results. The method used for faecal analysis followed Watts (1968), Hansson (1970), and Richards et al. (1984). Samples were grouped into batches, each batch comprising all the droppings collected from a given nest-box or Sherman trap in a given month. A total of 21 batches of droppings was examined; each batch was pooled homogenized, and a total of 5 slides was prepared; within each slide, a total of 100 fields of view was examined at 40×, recording the food remains present in each field. Food remains were identified with the aid of a reference collection. Pollen, spores, and remains of the bait were not recorded in droppings from Sherman traps.

The results revealed a basically herbivorous diet (Tab. 1), with a marked variation over the activity period, as summarized in figure 1. The fleshy fruits detected were mainly blackberry and apple, and to lesser amounts bilberry and rowan-berry. Nuts included acorns and hazelnuts. Leaves identified were mostly from *Rubus ulmifolius*; other species were *Quercus robur*, *Betula celtiberica*, and *Ilex aquifolium*. Flowers were not identified at the species level. Animal-prey remains were exclusively insects (hymenoptera, coleop-

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Table 1. Diet of the edible dormouse in the Montes do Invernadeiro: pooled results for all 21 batches of droppings. N = total number of remains of the food type detected. %F = percentage frequency (N as a percentage of total N).

Food type	N	%F
Fleshy fruit	2614	46.5
Nuts	2077	37
Leaves/flowers	449	8
Arthrópods	385	6.9
Fungi	63	1.1
Briophytes	34	0.5

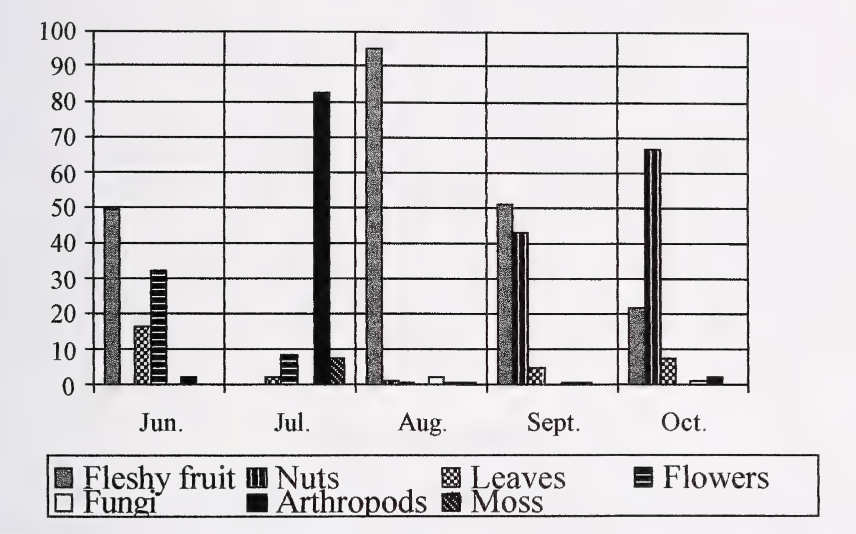


Fig. 1. Changes in the frequency of consumption of the different food types over the activity period (June–October). Values shown are frequencies of occurrence (number of batches of droppings containing that food type, as a percentage of the total number of batches in that month).

tera, and hemioptera), and/or arachnida. Fungus remains were mostly ascomycetes of the genus *Elaphomyces*. The consumption of moss was probably accidental.

These results are in accordance with previous reports. In Italy, Kahmann (1965) found that the June/July diet comprised plant remains, insects and *Rubus* flowers, whilst in July/August seeds of hornbeam, nuts, and blackberies. In Czechoslovakia, Holisova (1968) found that the early-summer diet comprised vegetative plant structures; in late-summer vegetative plant structures, fungi, hazelnuts, and dogwood fruits; and in autumn principally dogwood fruits, hawthorn fruits and sycamore seeds. In the Iberian Peninsula, Castroviejo et al. (1974) found that the June/July diet was comprised of insects, leaves, and fruits, the August diet leaves, fruit, and nuts, and the September/October diet fruit and nuts.

During May we did not find faeces either in nest-boxes or in traps. This suggests that in our study area the activity period does not begin until June, as has been reported for other regions (Kahmann 1965; Gaisler et al. 1977; Rodolfi 1994).

During September and particularly October (pre-hibernation period), the diet is dominated by nuts. This can be attributed to the need to accumulate the body fat required to survive the winter; indeed, their abundance may be an important determinant of population density (Vietinghoff-Riesch 1960; Castroviejro et al. 1974; Storch 1978).

We have not found any evidence of storage of food in larders, previously reported by Koenig (1960). However, food appears to have been Þ brought to and eaten in nest-boxes, which may be a predator-avoidance behaviour. Our results also indicate that fruits are eaten regardless of their degree of ripeness (bilberries in June and hazel nuts in August), as has been reported previously by Sykora (1970) and Rodolfi (1994).

An evidence of food preference was provided by wild apple: only a single apple tree is present in the study area, but during August this food item constituted a major part of the diet, and in some cases we can infer that the dormouse moved 200 m to reach the tree. This preference has been noted in previous studies (Thompson 1952; Morris and Hoodless 1992). It seems obvious that dormice actively select apples as a source of carbohydrates, once the reproductive period has finished.

The large amounts of arthropod remains detected in July may be a response to the high energy demand over the sexual activity, in view of the fact that no energy-rich plant foods are available at this time, as previously suggested by Franco (1990). We did not detect any evidence of vertebrate prey, as has been cited in previous studies (Vietinghoff-Riesch 1960; Storch 1978; Robel and Leitenbacher 1993).

The genus *Elaphomyces*, comprises fungi with below-ground fruiting bodies, implying that dormice must have dug in the soil to reach this food source. It is possible that this reflects deliberate searching; alternatively, and particularly during September and October, this food item may have been found during searching for suitable hibernation sites.

Results from September and October are similar to those obtained by analysis of stomach contents of individuals captured in the same area (Gigirey and Rey 1998); but faecal analysis gave lower nut estimates. This difference can be attributed to the efficiency of the edible dormouse in digesting nuts for conversion into body fat (Gebczynski et al. 1972), leading to under-estimation in faeces.

Acknowledgements

We thank Francisco de Diego Calonge, of the Real Jardín Botánico in Madrid, for help with identification of fungi, and the Servicio de Medio Ambiente of the Xunta de Galicia for facilitating our fieldwork. This work was financed by projects no. XUGA 20011B90 and XUGA 20011B96.

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Z. Säugetierkunde **64** (1999) 380–382
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MITTEILUNG DER GESELLSCHAFT

Protokoll über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. am 27. September 1999 im Bad Dürkheimer Haus, Bad Dürkheim

Der 1. Vorsitzende, Herr ERKERT, eröffnet die Versammlung um 16.10 Uhr.

1. Die Tagesordnung wird angenommen.

2. Herr SCHRÖPFER verliest den Bericht über das Jahr 1998. Auf Einladung der Herren Prof. Dr. S. C. KAREL STULIK, Prof. Dr. V. HANAK und Herrn Doz. Dr. LEO SIGMUND, Lehrstuhl für Zoologie, fand die 72. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde e. V. vom 20.–24. September 1998 an der Karls-Universität zu Prag statt. In 81 Vorträgen und Poster-Präsentationen zu den Schwerpunktthemen „Biodiversitätsforschung", „Morphologie und Phylogenie" und „Biologie der Insektivora und Chiroptera" sowie zu freien Themen bekamen ca. 120 Teilnehmer ein inhaltsreiches Programm geboten. Eine wissenschaftliche Exkursion galt dem Zoo von Dvur Kralove, eine weitere dem Thaya-Tal. Beide waren eine sinnvolle und anregende Ergänzung des Vortragsprogramms. Herr SCHRÖPFER spricht den Veranstaltern, ihren Mitarbeiterinnen und Mitarbeitern seinen herzlichen Dank für die Gastfreundschaft aus. Alle Teilnehmer werden diese Tagung, die im Rahmen des 650jährigen Jubiläums der ehrwürdigen Karls-Universität stattfand, in guter Erinnerung behalten.

   Die Preise des Poster-Wettbewerbs der Prager Tagung gingen an

   1. C. WEBER, K. KUGELSCHAFTER, R. FRANK: Spätsommerliches Erkunden von Baumhöhlenwinterquartieren durch juvenile Abendsegler (*Nyctalus noctula*),
   2. K. JOHANNESSON-GROSS: Zur Grabaktivität des Maulwurfs (*Talpa europaea*): Abmessungen von Erdhügeln und ihre Größenverteilung im Jahresverlauf.
   3. H. ANSORGE: Biologische Daten des Marderhundes aus der Oberlausitz.

   Den Fritz-Frank-Förderpreis erhielt Dipl.-Biol. Dr. SIMONE SOMMER für ihre Forschungen über die Populationsökologie und -genetik von *Hypogeomys antimena*, einer endemischen Nagerart im Trockenwald Westmadagaskars.

   Band 63 der Zeitschrift für Säugetierkunde erschien in sechs Heften mit insgesamt 384 Seiten. Er enthielt 30 wissenschaftliche Originalarbeiten, 16 wissenschaftliche Kurzmitteilungen, vier Mitteilungen der Gesellschaft und fünf Buchbesprechungen. Den beiden Schriftleitern und den Mitarbeitern des wissenschaftlichen Beirates wird ebenso gedankt wie dem Verlag.

   Außerdem wurde das Supplementheft herausgegeben, das über die wissenschaftlichen Beiträge der 72. Jahrestagung der Gesellschaft in Prag Auskunft gibt. Es enthält auf 69 Seiten 81 Kurzfassungen von 134 Autoren.

   Am 31. 12. 1998 hatte die Gesellschaft 601 Mitglieder.

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Durch Tod verlor die Gesellschaft folgende Mitglieder:

Prof. Dr. Walter Pflumm, Mitglied seit 1974
Herrn Hendrik van den Bergh, Mitglied seit 1973,
Herrn Walter Polzin, Mitglied seit 1930.

3. Herr Schröpfer erläutert den von Frau Kühnrich vorgelegten Kassenbericht und dankt der Schatzmeisterin für ihre umsichtige Arbeit.

4. Die Herren Bohlken und Schliemann haben die Kontounterlagen, der Gesellschaft in Hamburg geprüft und für korrekt befunden.

5. Die Anträge auf Entlastung der Schatzmeisterin und des Vorstandes werden bei vier Enthaltungen angenommen.

6. Die Herren Bohlken und Schliemann werden als Kassenprüfer für das Jahr 1999 einstimmig wiedergewählt. Beide sind mit der Wahl einverstanden.

7. Der Vorstand schlägt vor, die Mitgliedsbeiträge für das Jahr 2000 unverändert zu lassen. Die Anwesenden beschließen dies mit großer Mehrheit.

8. Die Mitgliederversammlung beschließt, die 74. Jahrestagung vom 24.–28. 9. 2000 gemeinsam mit der holländischen Säugetiergesellschaft VZZ in den Niederlanden abzuhalten. Der Tagungsort wird rechtzeitig mitgeteilt werden. Als Schwerpunktthemen sind vorgesehen „Meeressäugetiere", „Biologie und Schutz der Fledermäuse", „Soziobiologie, Sozioendokrinologie, Stress". Für das Jahr 2001 laden Herr Zeller und Herr Frädrich nach Berlin ein (75 Jahre DGS). Im Zusammenhang mit dem Tagungsinhalt wird die Frage erörtert, ob es sinnvoll ist, wie bisher drei Schwerpunktthemen zu benennen oder künftig nur zwei, wodurch den Freien Themen ein größerer Raum zukommen würde.

9. Herr Rehkämper stellt sein Konzept für die Arbeit der Tierschutzkommission vor. Zur Zeit ist vorgesehen, folgende Themen zu behandeln: Tierversuche, Tierschutz und Grundgesetz, Zootiere, Haustiere. In der anschließenden Diskussion wird deutlich, daß einige Mitglieder den Themenkreis erweitert sehen möchten, doch soll aus praktischen Gründen vorerst darauf verzichtet werden.
   Herr Pelz berichtet kurz über die Aktivitäten der Artenschutzkommission und weist auf die Notwendigkeit hin, den juristischen Status des Fischotters zu verändern. Herr Schröpfer gibt die Bildung einer Mustelidengruppe bekannt.

10. Da für eine intensive Diskussion der Fragen, die den künftigen Titel, das Format und Layout sowie den Inhalt der Zeitschrift für Säugetierkunde betreffen (englischer Untertitel oder Titel, Internationalisierung der Zeitschrift) die Zeit nicht mehr ausreicht, wird beschlossen, die Sitzung zu unterbrechen und die weitere Behandlung von TOP 10 am 28. 9. 1999 um 12.00 Uhr fortzuführen.

Die Sitzung endet um 18.50 Uhr.

Am folgenden Tag eröffnet der 1. Vorsitzende, Herr Erkert, die Fortsetzung der Versammlung um 12.15 Uhr.

Nach intensiver Diskussion über die Gestaltung der Zeitschrift für Säugetierkunde empfiehlt die Mitgliederversammlung mehrheitlich (34 Ja-Stimmen, 0 Gegenstimmen, 2 Enthaltungen), auf der nächsten Frühjahrssitzung des erweiterten Gesamtvorstandes die notwendigen Änderungen in einem „Gesamtpaket" einvernehmlich mit dem Verlag zu beschließen.

Die Mitgliederversammlung beschließt mit drei Enthaltungen, daß das Logo der Gesellschaft auf der Titelseite erscheinen soll.

Die Titelseite soll eine Abbildung tragen (angenommen bei 4 Gegenstimmen und einer Enthaltung).

Das Format der Hefte soll nur dann geändert werden (zweispaltiger Druck), wenn die Änderung kostenneutral ausfällt (16 Ja-Stimmen, 12 Gegenstimmen, 7 Enthaltungen).

Es wurde angeregt, im Hinblick auf eine Abbildungskartei für die Titelseite der Zeitschrift im Jahr 2001 in Berlin eine Bilderausstellung durchzuführen.

Die Sitzung endet um 13.18 Uhr

Prof. Dr. H. Erkert (1. Vorsitzender)	Prof. Dr. R. Schröpfer (Geschäftsführer)	Dr. H. Frädrich (Schriftführer)

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Buchbesprechungen

Wójcik, J. M.; Wolsan, M. (eds.) (1998): **Evolution of Shrews.** Bialowieza: Mammal Research Institute, Polish Academy of Sciences. Hardcover, 458 pp. num. figs. and tabs. US $ 38.–. ISBN 83-907521-0-7.

The aim of this book is to review recent knowledge on the evolutionary biology of shrews and to point out current problems. This comprehensive multi-authored compilation is presented in altogether 13 chapters, well-ordered, dealing with several aspects, and written by internationally well-known experts in their fields. Following introductory editorial remarks, including brief conclusions of the different themes, the first chapter (Reumer) deals with the classification of these special and species-rich insectivores. Here, in addition to older opinions, a new approach is presented. Accordingly, certain extinct genera with zygomatic arches and further skull characters, formerly ranked as subfamily, are now classified in the family Heterosoricidae, whereas the vast majority of fossil and recent shrews lacking zygomatic arches and attributed with other distinct skull peculiarities is supplemented under the family Soricidae with 5 subfamilies. The numerous genera and species of the subfamily Soricinae are further assigned to 7 tribes. Most of the other authors of this book follow strictly these conclusions. The next chapters deal with the history of shrews documenting the situation in Europe (Rzebik-Kowalska), Asia (Storch, Qiu, Zazhigin), Africa (Butler), and North America (Harris). No fossils were recorded from South America and only a few *Cryptotis*-species are recognized from northern parts of this continent in recent distribution. Thus, late immigration from the north appears probable. According to the fossil documentation Heterosoricidae were obviously distributed from Middle and Late Eocene to Middle and Late Miocene in North America respectively Europe and from Early Oligocene to Late Miocene in Asia, whereas Soricidae were first recognized from Early Oligocene in Europe (with the Soricinae being "older" than Crocidurinae), from Late Oligocene in North America, and from Early Miocene to present in Asia (with the Soricinae and Crocidurinae likewise since Middle Miocene). The history in Africa is poorly documented for only some Soricidae from the Middle Miocene on. This is discussed in connection with the origin of shrews on land masses of the northern hemisphere and the fact that Tertiary Africa and Arabia were separated from Eurasia by the Tethys Sea. A land bridge connecting Arabia with southeastern Asia first emerged during Middle Miocene. Thus, since these eras immigrations of shrews and faunal exchanges between Africa and Eurasia are supposed. A further chapter (Dannelid) deals with dentition, especially that of extant genera but data on extinct forms are included. Both ecological and phylogenetical conclusions are presented very convincingly in detail and in overview as well. Evolutionary and several convergent adaptive trends in Soricidae are focused concerning tooth reductions, tooth modification, and pigmentation. Two subsequent chapters are devoted to the chromosomal configuration in shrews. At first (Zima, Lukáčová, Macholán) a general overview documents present knowledge on 52 species of Crocidurinae with diploid numbers ranging from 22 to 60 and 45 species of Soricinae with a range from 20 to 68. These are commented on in their basic karyotypes and intra- as well as interspecific variations. The unusual heterosomal system known from 8 *Sorex* species is also stressed with males possessing XY_1Y_2, while females have the normal XX. Then, a special chapter (Searle, Wójcik) is centered on the phenomenal chromosomal variability of the Robertsonian type in *Sorex araneus.* This species varies remarkably in diploid number from 20 to 33 at a constant fundamental number of 40. Several karyotypic races are characterized and possible phylogenetic relationships between these are reconstructed with special emphasis on interracial hybrid zones. Two consecutive chapters are devoted to results obtained from molecular methods. Protein variation (Ruedi) is focused at the specific and generic level of some Crocidurinae and Soricinae, and mt DNA diversities (Hausser, Fumagalli, Taberlet) in shrews are discussed as an additive tool for phylogenetic reconstruction among western European species and within karyotypic races of the *S. araneus* group. Physiological characteristics are also presented in a review (Taylor) concerning evolutionary patterns and energetics. Here, the generally higher metabolic rate levels and strict homeothermy of soricines are contrasted with lower rates in crocidurine species and their ability to enter torpor. These generally different adaptations are discussed in connection with

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geopraphical origin, phylogeny, environmental adaptation, reproductive traits, and other biological parameters. The two last chapters are devoted to ethology, e. g., social organisation (Rychlik) and mating biology (Stockley, Searle) documented as results from observations in the field and in captivity as well. Four social systems are described in extant species in relation to communication, mating systems, rearing of young, predation avoidance, habitat use, etc. The mating systems are documented as different adaptive radiations concerning oestrus, mating behaviour, dispersal and spatial organization. Finally, an appendix (Wolsan, Hutterer) offers an updated list and systematics of the known 335 species in 23 genera with their common names, distribution, and brief habitat characterisation. A taxonomic index is also added.

This book certainly deserves close attention not only by specialists but also mammalogists in general. It contains a very large amount of details on the biology of these mammals and many aspects to evaluate and understand phenomena and characteristics. It is also intended to stimulate further research.

D. Kruska, Kiel

Klima, M. (1999): **Development of the Cetacean Nasal Skull**. In: Advances in Anatomy, Embryology and Cell Biology, Vol. 149. Berlin, Heidelberg, New York: Springer-Verlag. Softcover, 143 pp., 68 illustrations, 1 table. DM 186,– / US$ 119,–. ISBN 3-540-64996-4.

The author of this book on the nasal skull of the Cetacea was able to investigate embryological material from seven species of the Odontoceti (toothed whales) and three species of the Mysticeti (baleen whales). Because of the general rarity of appropriate cetacean material in collections around the world, the reader has to agree with the author's self-confident statement that his "contribution, even though incomplete, is probably the most thorough treatment of the topic for some time to come".

After a section dealing with the prenatal differentiation of the nasal skull, emphasis is paid to changes in position and form of structures in this part of the cranial skeleton, followed by an interspecific comparison of structures in embryonic and adult Cetacea. These sections are illustrated by very informative drawings and micrographs. Relevant structures are marked exclusively by abbreviations, which are listed and explained in a table at the beginning of the book. To appreciate the illustrations properly, the reader has to thumb through page upon page, a rather cumbersome procedure!

In the subsequent section the author deals with the question why the nostrils in whales "lie in the highest point of the cetacean body", but in the fossil ichthyosaurus the "nostrils were situated laterally on the skull, directly in front of the eyes". This difference may be related to the ventro-dorsal movement of the cetacean fluke and the right-left motion of the ichthyosaurous tail.

In a final section Klima comments on the systematics within the order Cetacea. His findings do not contradict the modern view that sperm whales have to be classified in a separate subfamily (Physeteroidea) from the other toothed whales, the Delphinoidea, and the baleen whales, Balaenopteroidea. The illustrations for this important section are taken from previous papers (Klima 1995 and Milinkovitch, 1995). The editors should have marked homologous anatomical structures by clear signatures (Fig. 67) and should have removed redundant abbreviations (Fig. 68).

P. Langer, Gießen

Instructions to Authors

Submission and Acceptance of Manuscripts: Manuscripts for publication should be sent to the managing editor, Prof. Dr. D. Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel, Germany, e-mail: dkruska@ifh.uni-kiel.de. Acceptance of the manuscript follows the bylaws of the German Society for Mammalogy (Deutsche Gesellschaft für Säugetierkunde). Receipt of the manuscript will be confirmed immediately by mail, and as soon as the peer reviews are received the authors will be informed concerning the decision for acceptance.

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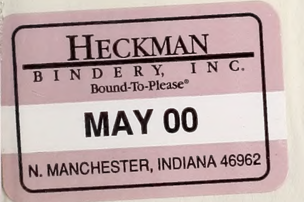
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